

# Open Research Online

---

The Open University's repository of research publications  
and other research outputs

## Human and climate impacts on tropical Andean ecosystems

### Thesis

#### How to cite:

Williams, Joseph James (2011). Human and climate impacts on tropical Andean ecosystems. PhD thesis The Open University.

For guidance on citations see [FAQs](#).

© 2011 The Author

Version: Version of Record

---

Copyright and Moral Rights for the articles on this site are retained by the individual authors and/or other copyright owners. For more information on Open Research Online's data [policy](#) on reuse of materials please consult the policies page.

---

[oro.open.ac.uk](http://oro.open.ac.uk)



# **Human and Climate Impacts on Tropical Andean Ecosystems**

A thesis presented for the degree of Doctor of Philosophy

by

**Joseph James Williams**

B.Sc. Hons (University of Southampton)

May 2011

Department of Earth and Environmental Sciences

Center for Earth, Planetary, Space and Astronomical Research

The Open University

The United Kingdom



**THESIS CONTAINS  
CD/DVD**

Population growth and predicted global climate change are applying new, and increasing, pressure to mountain environments, but the consequences of these changes upon the biodiverse and vulnerable Tropical Andean ecosystems are poorly understood. This thesis explores past human-climate-ecosystem interactions using multi-proxy palaeolimnological investigations (fossil pollen, spore, charcoal and Chironomidae (midges); elemental abundance, colour spectra and magnetic susceptibility) of two sites in the eastern Bolivian Andes (Lake Challacaba and Laguna Khomer Kocha Upper) over the last c. 18,000 years. During the deglaciation and Holocene, ecosystems were exposed to varying climatic stress levels, and pressures imposed by the development of human cultures.

Examination of preserved ecological assemblages, including the first assessment of subfossil central Andean Chironomidae, reveals ecosystem sensitivity to changes in temperature, moisture, fire regime, lake level, nutrients and salinity. Charcoal analysis from Laguna Khomer Kotcha Upper reveals changes in burning at c. 14,500, 10,100 and 6,400 cal yr BP. Concomitant palynological shifts shows climatically controlled fire regime was a transformative agent of Andean vegetation, particularly for the threatened, high elevation, *Polylepis* woodlands. Pollen and geochemical data from Lake Challacaba indicate two periods of aridity (c. 4,000–3,370 and 2,190–1,020 cal yr BP), these broadly correlated to El Niño/Southern Oscillation variations. Increased *Sporormiella* abundance after c. 1,340 cal yr BP indicate changes in trade-route use and agricultural practices; demonstrating human adaptation to environmental change and interconnectivity to Tiwanaku and Inca civilizations.

The long-term response of the terrestrial and aquatic ecosystems, reconstructed from these lakes, has provided insights into how Tropical Andean ecosystems may respond to future changes in temperature, precipitation and human interference. The palaeoenvironmental data has implications for conservation management; it indicates that spatial and temporal variations in site sensitivity, exposure and resilience should be

## *Abstract*

assessed, and that planting strategies should mimic the present day natural patchy distribution of *Polylepis* woodlands.

## Acknowledgments

---

First of all I wish to thank my supervisors Will Gosling, Angela Coe and Steve Brooks for their encouragement, guidance and support over the past three and a half years. I just hope I manage to retain even a fraction of all the knowledge they have imparted. Will without doubt warrants special thanks. Not only are you an excellent supervisor, but also one of the few scientists who somehow is able to see the big picture in the midst of all the hundreds of thousands of pollen grains, charcoal fragments, and chironomid remains. Above this, you are also the person who first introduced me to Bolivia; albeit via a plate of gherkins, phony police and U.S. customs officials. I hope your first experiences of supervision have not put you off future students.

Thank you to all the great people of Cochabamba who helped with transport, site access, accommodation or just generally preventing us from walking into the wrong neighbourhoods. I hope that this work manages to portray what a fantastic country Bolivia is. In particular, Eric Martinez Costas, Lydia Meneses Lizarazu, the Museo Historia Natural 'Noel Kempff Mercado' in Santa Cruz, and the Jardin Botanico 'Martin Cardenas' in Cochabamba. Thanks also to GNS Science Wairakei Research Centre and staff, for giving me desk space for the two months I spent in New Zealand.

To the people who have had to be put up with me in the various labs, student offices or fieldwork, I'm sorry. Thanks to the folks of RocSoc and Touch Rugby Club for the countless weekends away, ski trips, annual dinners, snow days, spider-vac tests, Friday beers, risky nights, BBQ's, pub Mercredi's and, most of all, doing things more stupid than me. For somehow making sure things turned out OK in the end, I owe a huge amount to many people, particularly Alison (shouty), Gaz, Josh, Lottie, Maca, Nats, Pierre, Sammy, Trish and Wes. Back home in Leicester; Joey, Dave, Josh and Dan, and in Southampton; Mousey.

Thanks must also go to my family around the globe, particularly mum and dad. You supported me through all the undergrad years, let me disappear to all sorts of foreign

## *Acknowledgments*

countries, and not once have bugged me to get a proper job. Tamsin, Juliet, Sarah and Clare, I hope I get to see a lot more of you all in the coming years. Nana, for as long as I can remember you've taken an interesting in everything I do and shared in my love for the natural world. Simply put, you are all amazing and I'm privileged to be part of this family.

Finally, I wish to thank Saskia van Manen. Even though sometimes the whole planet was between us (literally), your love, support and unwavering encouragement kept me going through the mad last few years. Maybe one day the Dr-Dr combo might win us an upgrade!

Table of contents

**Abstract** ..... ii

**Acknowledgments** ..... iv

**Table of contents** ..... vi

**List of figures** ..... xii

**List of tables** ..... xv

**List of plates** ..... xvi

**Previously published material** ..... xvii

**Chapter 1) Introduction** ..... 1

    1.1 The Topical Andes ..... 1

        1.1.1 *Geographical location and setting* ..... 2

        1.1.2 *Modern ecology* ..... 5

        1.1.3 *Environmental changes* ..... 13

        1.1.4 *Human occupation* ..... 16

    1.2 Palaeoecology: tracing human and climate ecosystem impacts ..... 23

    1.3 Thesis rationale and objectives ..... 25

    1.4 The Cochabamba Basin, Bolivia ..... 27

        1.4.1 *Geographical location and setting* ..... 27

        1.4.2 *Modern ecology* ..... 31

        1.4.3 *Climate* ..... 32

        1.4.4 *Human occupation* ..... 34

    1.5 Thesis structure and layout ..... 35

**Chapter 2) Study sites** ..... 37

    2.1 The Vacas Lake District - Lake Challacaba ..... 37

        2.1.1 *Geographical location and setting* ..... 37

        2.1.2 *Modern ecology* ..... 40

        2.1.3 *Climate* ..... 42

        2.1.4 *Human occupation* ..... 43

    2.2 Laguna Khomer Kotcha Upper ..... 45

        2.2.1 *Geographical location and setting* ..... 45

2.2.2	<i>Modern ecology</i>	48
2.2.3	<i>Climate</i>	51
2.2.4	<i>Human occupation</i>	53
2.3	Conclusions	54
<b>Chapter 3) Field and laboratory methods and analytical techniques</b>		55
3.1	Lake observations and data recording	55
3.2	Lake sediment coring procedure	56
3.2.1	<i>Long core</i>	56
3.2.2	Short core (sediment/water interface)	57
3.3	Sample logging, documentation and subsample extraction	59
3.3.1	<i>Core splitting</i>	59
3.3.2	Description and cataloguing	59
3.4	Analysis of ecological proxies	62
3.4.1	<i>Fossil pollen and spore</i>	62
3.4.2	Charcoal	67
3.4.3	Chironomidae	71
3.5	Chronological framework	78
3.6	Analysis of geochemical and physical properties	80
3.6.1	<i>Magnetic susceptibility</i>	80
3.6.2	<i>Spectral / colour</i>	85
3.6.3	<i>Elemental: carbon, sulphur and nitrogen</i>	88
3.7	Statistical functions and software packages	90
<b>Chapter 4) Four thousand years of environmental changes and human activity in the Cochabamba Basin, Bolivia</b>		92
4.1	Abstract	92
4.2	Introduction	93
4.2.1	<i>Regional setting</i>	94
4.2.2	<i>Study sites</i>	98
4.3	Methods	98
4.4	Results	101
4.4.1	<i>Chronology</i>	101
4.4.2	<i>Sediments</i>	103

4.4.3	<i>Physical and chemical properties</i>	103
4.4.4	<i>Pollen, spore and charcoal zone description</i>	105
4.5	Environmental reconstruction and discussion	110
4.5.1	<i>Late Holocene climatic changes: moisture balance fluctuations</i>	110
4.5.2	<i>Changing human activity</i>	114
4.5.3	<i>Fire history</i>	116
4.5.4	<i>The Polylepis woodland / grassland matrix</i>	117
4.6	Conclusions	118
4.7	Acknowledgments	119
<b>Chapter 5)</b>	<b>The sensitivity of eastern Andean vegetation to climate and fire</b>	<b>120</b>
5.1	Abstract	120
5.2	Introduction	121
5.3	Study Location	123
5.4	Material and methods	127
5.5	Results	129
5.5.1	<i>Chronology and sediment description</i>	129
5.5.2	<i>Physical and chemical properties</i>	131
5.5.3	<i>Zonation</i>	132
5.5.4	<i>Pollen, spore and charcoal zone description</i>	132
5.5.5	<i>Ordination</i>	137
5.6	Environmental reconstruction and discussion	138
5.6.1	<i>Deglacial vegetation dynamics</i>	138
5.6.2	<i>Early and mid-Holocene climate variation</i>	142
5.6.3	<i>Formation of the modern vegetation structure</i>	145
5.6.4	<i>Potential anthropogenic impacts</i>	146
5.7	Conclusions	147
5.8	Acknowledgments	148
<b>Chapter 6)</b>	<b>On the identification and interpretation of Late Pleistocene and Holocene Chironomidae from the eastern Bolivian Andes</b>	<b>149</b>
6.1	Abstract	149
6.2	Introduction	150
6.3	Regional setting and study sites	153



6.3.1	<i>Lake Challacaba (Vacas Lake District)</i>	155
6.3.2	<i>Laguna Khomer Kocha Upper (Cordillera el Ronco)</i>	157
6.4	Material and methods	160
6.5	Results	161
6.5.1	<i>Taxonomic notes</i>	161
6.5.2	<i>Chironomid stratigraphy</i>	165
6.6	Discussion	172
6.6.1	<i>Lake Challacaba</i>	172
6.6.2	<i>Laguna Khomer Kocha Upper</i>	175
6.6.3	<i>Application considerations</i>	176
6.7	Conclusions	177
6.8	Acknowledgments	178
<b>Chapter 7) Palaeoecology and conservation: a case study from the Eastern</b>		
<b>Cordillera of Bolivia</b>		
7.1	Threats to the ecological value of the Tropical Andes	179
7.1.1	<i>Climate threats</i>	179
7.1.2	<i>Human threats</i>	180
7.2	Conservation insights from palaeoecology	182
7.3	The Cochabamba Basin, Eastern Bolivian Cordillera	184
7.3.1	<i>Local environmental concerns</i>	184
7.3.2	<i>Local palaeoecological records</i>	187
7.4	Vulnerabilities	189
7.4.1	<i>Exposure</i>	189
7.4.2	<i>Sensitivity</i>	192
7.4.3	<i>Resilience</i>	193
7.5	Implications	195
7.5.1	<i>Conservation and vulnerability</i>	195
7.5.2	<i>The future of Polylepis woodlands</i>	196
7.6	Conclusions	198
<b>Chapter 8) Conclusions</b>		
8.1	Summary of thesis rationale and objectives	199
8.2	Specific research findings	201

8.2.1	<i>The scale and impact of climatic adjustments</i>	201
8.2.2	<i>Pre-Columbian populations</i>	203
8.2.3	<i>The natural history of the Polylepis woodlands</i>	205
8.3	Suggestions for future work	207
8.3.1	<i>Data collection</i>	207
8.3.2	<i>Data application</i>	209
<b>References</b>		210
<b>Appendix A1). Initial core descriptions</b>		246
A1.1	Description methodology and key	246
A1.2	Lake Challacaba	248
A1.3	Laguna Khomer Kocha Upper	256
<b>Appendix A2) Analytical protocols</b>		267
A2.1	pH, conductivity and temperature analysis – Hanna 991300 probe	267
A2.1.1	<i>pH</i>	267
A2.1.2	<i>Conductivity (mS/cm)</i>	267
A2.1.3	<i>Calibration</i>	267
A2.2	Core tube splitting	268
A2.2.1	<i>Set up</i>	268
A2.2.2	<i>Cutting</i>	268
A2.2.3	<i>Splitting the sediments</i>	268
A2.3	Photographic set up	269
A2.4	Fossil pollen and spore analysis	270
A2.4.1	<i>Sample set up</i>	270
A2.4.2	<i>Solution and removal of carbonates and humic compounds</i>	270
A2.4.3	<i>Solution and removal of silicates and sulphides</i>	272
A2.4.4	<i>Removal of cellulose and polysaccharides – acetylation</i>	273
A2.4.5	<i>Slide preparation</i>	273
A2.5	Charcoal analysis	274
A2.5.1	<i>Sample set up</i>	274
A2.5.2	<i>Wet lab preparation</i>	274
A2.6	Subfossil chironomid analysis	275
A2.6.1	<i>Sample set up</i>	275

A2.6.2	<i>Wet lab preparation</i> .....	275
A2.6.3	<i>Picking and mounting procedure</i> .....	275
A2.7	Elemental determination .....	276
A2.7.1	<i>Instrumentation</i> .....	276
A2.7.2	<i>Measurement protocol</i> .....	277
<b>Appendix A3)</b>	<b>Bolivian Lake Sediment Data</b> .....	<b>281</b>
A3.1	Radiometric dates .....	281
A3.1.1	<i>Sample pre-treatment and analysis</i> .....	281
A3.1.2	<i>Reported results</i> .....	282
A3.2	Geochemical and physical data .....	284
A3.3	Ecological proxies data .....	292
A3.3.1	<i>Pollen and spore</i> .....	292
A3.3.2	<i>Charcoal</i> .....	292
A3.3.3	<i>Chironomid</i> .....	292
A3.3.4	<i>Ordination</i> .....	295
<b>Appendix A4)</b>	<b>Identified ecological remains</b> .....	<b>298</b>
A4.1	Pollen, spore and algal types .....	298
A4.2	Chironomid types .....	300

## List of figures

<b>Figure 1.1</b> Extent of the South American Topical Andes and major climate systems. .	2
<b>Figure 1.2</b> Digital shaded relief map and elevational cross-section of Bolivia. ....	4
<b>Figure 1.3</b> South American Biomes. As defined by the WWF. ....	5
<b>Figure 1.4</b> Ecoregions of Bolivia and southern Peru. As defined by the WWF. ....	6
<b>Figure 1.5</b> <b>A)</b> Yungas cloud forest and <b>B)</b> Central Andean Puna ecoregions. ....	8
<b>Figure 1.6</b> <i>Polylepis</i> woodlands of Cochabamba, Bolivia. <b>A)</b> Setting. <b>B)</b> Growth structure. <b>C)</b> Bark adaptations. ....	10
<b>Figure 1.7</b> Schematic of <i>Polylepis</i> fragmentation drivers. <b>A)</b> Natural. <b>B)</b> Anthropogenic . ....	11
<b>Figure 1.8</b> Natural limits of <i>Polylepis</i> in modern day Bolivia. <b>A)</b> Vegetation type boundaries. <b>B)</b> Limiting factors. ....	16
<b>Figure 1.9</b> Basic cultural chronology and inferred climatic conditions of the Bolivian Altiplano. ....	19
<b>Figure 1.10</b> Territorial spheres of the Inca and Tiwanaku. ....	20
<b>Figure 1.11</b> Bird species richness and endemism along an elevational transect in the Carrasco National Park, Cochabamba, Bolivia. ....	23
<b>Figure 1.12</b> The Cochabamba Basin with study locations marked. ....	28
<b>Figure 1.13</b> Monthly average climate data for the Cochabamba basin, 2000-2009 inclusive. ....	33
<b>Figure 2.1</b> The Vacas Lake District and known <i>Polylepis</i> woodlands. ....	38
<b>Figure 2.2</b> Composite photograph of Lake Challacaba, Vacas Lake District. ....	39
<b>Figure 2.3</b> Map of Lake Challacaba and local topographic features. ....	40
<b>Figure 2.4</b> Monthly average climate data for the Vacas Lake District: Meteorological and interpolated. ....	43
<b>Figure 2.5</b> Map of the Khomer Kocha area and local features. ....	46
<b>Figure 2.6</b> Map of the Khomer Kocha Lagunas (Upper and Lower). <i>Polylepis</i> woodlands shown. ....	46
<b>Figure 2.7</b> Laguna Khomer Kocha Upper. ....	47
<b>Figure 2.8</b> <i>Polylepis</i> woodlands local to Laguna Khomer Kocha Upper. ....	51

<b>Figure 2.9</b> Monthly average climate data for Laguna Khomer Kocha Upper. Interpolated data. ....	52
<b>Figure 3.1</b> Coring set up and equipment. <b>A)</b> Long core. <b>B)</b> Short core. <b>C-D)</b> Platform...	58
<b>Figure 3.2</b> Core photographic set up. ....	61
<b>Figure 3.3</b> Morphology of pollen and spore. <b>A)</b> <i>Polylepis/Acaena</i> . <b>B)</b> <i>Podocarpus</i> . <b>C-)</b> <i>Trilete spore</i> . <b>D)</b> <i>Poaceae</i> . ....	63
<b>Figure 3.4</b> Conceptual model of climate-vegetation-human interactions. ....	64
<b>Figure 3.5</b> Relationship between charcoal particle size and distance before deposition. <b>A)</b> Conceptual. <b>B)</b> Modeled (based on 3 ms <sup>-1</sup> wind speed). ....	68
<b>Figure 3.6</b> Charcoal morphotypes. <b>A)</b> Type 1. <b>B)</b> Type 2. ....	70
<b>Figure 3.7</b> Chironomid drawings . <b>A)</b> Life cycle. <b>B)</b> Larva. ....	72
<b>Figure 3.8</b> Morphology of chironomid larvae head capsules. <b>A)</b> <i>Parachironomus</i> . <b>B)</b> Orthocladinae. <b>C-)</b> <i>Tanytarsini</i> . <b>D)</b> Tanypodinae. ....	74
<b>Figure 3.9</b> Conceptual model of the relationship between taxonomic resolution and palaeoenvironmental information obtained. ....	76
<b>Figure 3.10</b> Outcome types of taxonomic errors. ....	77
<b>Figure 3.11</b> Conceptual diagrams of the four types of magnetic behaviour. ....	81
<b>Figure 3.12</b> Bartington MS2 Susceptibility System. ....	82
<b>Figure 3.13</b> Measurement procedure for the Bartington MS2 Susceptibility System....	83
<b>Figure 3.14</b> Spectral analysis procedure. <b>A-B)</b> Scanning layout. <b>C)</b> Analysis screenshot. ....	87
<b>Figure 3.15</b> Measurement procedure for the LECO CNS-2000 elemental analyser. ....	90
<b>Figure 4.1</b> Study site location. <b>A)</b> Cochabamba Basin. <b>B)</b> Vacas Lake District. <b>C)</b> Lake Challacaba. <b>D)</b> Lake Challacaba composite photograph. ....	97
<b>Figure 4.2</b> Age-depth curve for Lake Challacaba sediments. ....	102
<b>Figure 4.3</b> Physical, chemical properties and lithology of the Lake Challacaba sediments cores. ....	104
<b>Figure 4.4</b> Stratigraphic diagrams for Lake Challacaba. <b>A)</b> Pollen sum taxa and total concentration. <b>B)</b> Aquatic taxa, spores, algae and charcoal. ....	107
<b>Figure 4.5</b> Results of NMDS for Lake Challacaba. <b>A)</b> Ordination plot. <b>B)</b> Axis 1 and 2 and rate of change against time. ....	110

**Figure 5.1** Study site location. **A)** Cochabamba Basin. **B)** Laguna Khomer Kocha area.  
**C)** Laguna Khomer Kocha Upper and Lower. .... 125

**Figure 5.2** Laguna Khomer Kocha Upper and surrounding landscape. .... 126

**Figure 5.3** Age-depth curve and physical, chemical properties and lithology of the  
Laguna Khomer Kocha Upper sediments cores. .... 131

**Figure 5.4** Stratigraphic diagrams for Laguna Khomer Kocha Upper. **A)** Pollen sum  
taxa. **B)** Aquatic taxa, spores, algae, charcoal, total concentration, taxa richness and  
rate of change. Sajama ice core data also shown. .... 135

**Figure 5.5** Results of DCA for Laguna Khomer Kocha Upper (axis 1 and 2). .... 137

**Figure 5.6** Stratigraphic diagrams for Laguna Khomer Kocha Upper. Physical,  
chemical properties and charcoal. Sajama ice core data also shown. .... 138

**Figure 6.1** Study site locations. **A)** Cochabamba Basin. **B)** Lake Challacaba  
bathymetry. **C)** Laguna Khomer Kocha Upper bathymetry. .... 154

**Figure 6.2** Age-depth curves and lithology. **A)** Lake Challacaba. **B)** Laguna Khomer  
Kocha Upper. .... 158

**Figure 6.3 A-B)** Line drawings and photographs of key subfossil chironomid head  
capsules from Lake Challacaba and Laguna Khomer Kocha Upper. .... 162

**Figure 6.4** Palaeolimnological data for Lake Challacaba. **A)** Subfossil chironomid  
concentration data. **B)** Subfossil chironomid percentage data. **C)** Summary pollen,  
spore, algal, charcoal and geochemical/physical data. .... 166

**Figure 6.5** Palaeolimnological data for Laguna Khomer Kocha Upper. **A)** Subfossil  
chironomid concentration data. **B)** Subfossil chironomid percentage data. **C)**  
Summary pollen, spore, algal, charcoal and geochemical/physical data. .... 170

**Figure A2.1** Fossil pollen preparation tick sheet. .... 278

**Figure A2.2** Fossil pollen count sheet. .... 279

**Figure A2.3** Subfossil chironomid count sheet. .... 280

**List of tables**


---

<b>Table 1.1</b> Distribution of <i>Polylepis</i> species number and endemics. ....	9
<b>Table 1.2</b> Location details of the lakes visited for this study. ....	31
<b>Table 3.1</b> Methods and instrumentation used in measure lake variables. ....	55
<b>Table 3.2</b> Example applications of palaeo chironomid studies. ....	73
<b>Table 3.1</b> Software packages and functions applied in this study. ....	91
<b>Table 4.1</b> Radiocarbon dates and calibrated ages for Lake Challacaba. ....	102
<b>Table 5.1</b> Radiocarbon dates and calibrated ages for Laguna Khomer Kocha Upper. ..	130
<b>Table 6.1</b> Modern chironomid taxa collected from three major hydro-ecoregions of eastern Bolivia and the Altiplano. ....	152
<b>Table A1.1</b> Key to sediment composition codes used in core profile logs. ....	246
<b>Table A1.2</b> Key to sediment colour codes used in core profile logs. ....	247
<b>Table A2.1</b> Photographic methodologies tested. ....	269
<b>Table A2.2</b> Mean values for the in-house standard during elemental analysis. ....	277
<b>Table A3.1</b> Reported <sup>14</sup> C dates and calibrations. ....	283
<b>Table A3.2</b> Full geochemical and physical data for Lake Challacaba. ....	284
<b>Table A3.3</b> Full geochemical and physical data for Laguna Khomer Kocha Upper. ....	288
<b>Table A3.4</b> Full charcoal data for Lake Challacaba. ....	293
<b>Table A3.5</b> Full charcoal data for Laguna Khomer Kocha Upper. ....	294
<b>Table A3.6</b> Ordination data for Lake Challacaba. ....	296
<b>Table A3.7</b> Ordination data for Laguna Khomer Kocha Upper. ....	297
<b>Table A4.1</b> Spore and algal taxa identified from the sediment cores. ....	298
<b>Table A4.2</b> Pollen taxa identified from the sediment cores. ....	299
<b>Table A4.3</b> Chironomid taxa identified from Lake the sediment cores. ....	300

***List of plates***

---

---

<b>Plate A1.1 A-H)</b> Initial core description for Lake Challacaba. ....	248
<b>Plate A1.2 A-K)</b> Initial core description for Laguna Khomer Kocha Upper. ....	256



## ***Previously published material***

---

I confirm that following chapters have been previously published or submitted for publication.

***Chapter 4, "Four thousand years of environmental change and human activity in the Cochabamba Basin, Bolivia", has already been published separately as the following journal article:***

**Williams, J.J., Gosling, W.D., Coe, A.L., Brooks, S.J. and Gulliver, P.**

Four thousand years of environmental change and human activity in the Cochabamba Basin, Bolivia.

*Quaternary Research* (Online) DOI: 10.1016/j.yqres.2011.03.004

***Chapter 5, "The sensitivity of eastern Andean vegetation to climate and fire" has been submitted for publication separately:***

**Williams, J.J., Gosling, W.D., Brooks, S.J., Coe, A.L. and Xu, S.**

The sensitivity of eastern Andean vegetation to climate and fire.

*Palaeogeography, Palaeoclimatology, Palaeoecology* (Submitted April 20, 2011)

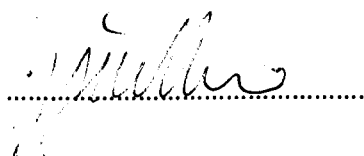
***Chapter 6, "On the identification and interpretation of Late Pleistocene and Holocene Chironomidae from the eastern Bolivian Andes", has been submitted for publication separately:***

**Williams, J.J., Brooks, S.J and Gosling, W.D.**

On the identification and interpretation of Late Pleistocene and Holocene Chironomidae from the eastern Bolivian Andes

*Journal of paleolimnology* (Submitted April 20, 2011; Under review 27 April, 2011)

Signed: .....



Date: .....

22<sup>nd</sup> September 2011



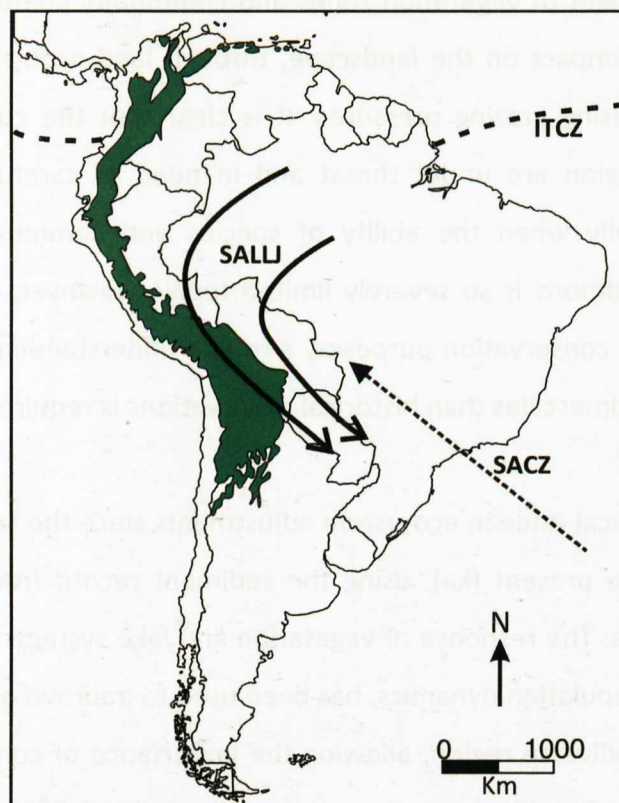
### **1.1) The Tropical Andes**

The highly diverse ecosystems of the elevated Tropical Andes are vulnerable because of increasing human occupation of the area and predicted future climate change (Cincotta et al., 2000; Malcolm et al., 2006; Myers et al., 2000). Narrow vertical species ranges in high elevation sites (>2000 metres above sea level (m asl)) means that even small variations in temperature and precipitation can result in considerable species movement. The sensitivity and diversity of Tropical Andean vegetation, together with the complex topography of the Andean valleys and ridges, typically of elevations 2500–4500 m asl, allows continuous montane forests to be separated from grassland and bare rocky peaks by just a few tens of kilometres laterally. Despite the relative short lateral and vertical distances, the adjustment of vegetation zones and community composition is restricted by increasing human impact on the landscape, through land acquisition, conversion to agriculture and increasing grazing pressures. It is clear that the current status of the ecosystems in the region are under threat and in need of careful conservation and management, especially when the ability of species and communities to shift with changing climatic conditions is so severely limited today. However, in order to provide information useful for conservation purposes, a robust understanding of an ecosystem's response over longer timescales than historical observations is required.

This thesis traces Tropical Andean ecosystem adjustments since the last glacial period, 18 thousand years before present (ka), using the sediment record from two lakes in the eastern Bolivian Andes. The response of vegetation and lake systems to climatic changes and shifts in human population dynamics, has been used to improve our understanding of the threats to this biodiverse region, allowing the importance of controlling factors and the spatial and temporal scales they operate on to be assessed. This examination of past human and climate impacts in the Tropical Andes provides evidence of how these ecosystems may react to future predicted changes (see Section 1.3 for specific objectives).

### 1.1.1) Geographical location and setting

The Tropical Andes biodiversity hotspot spans an area of 1,500,000 km<sup>2</sup> from Venezuela in the north to Argentina in the south (Figure 1.1; [www.conservationinternational.org](http://www.conservationinternational.org)). The hotspot covers elevations from as low as 500 m asl and follows the tropical portion of the Andes mountain chain, the longest continental range in the world, extending ~8000 km through the continent of South America (Murray et al., 2010). Uplift of the Andes is in association with the convergence and subsequent subduction of the Nazca tectonic plate under the South American plate, and has resulted in the highest plateau on Earth today that is formed at a noncollisional plate boundary (Gregory-Wodzicki, 2000; Montgomery et al., 2001). The uplift history of the Andes Cordillera (mountain chain/range) is varied and complex along its length (see Hoorn et al., 2010), but the Central Andes domain is considered to have been <30% of its current elevation by c. 25–14 million years ago (Ma) (Gregory-Wodzicki, 2000; Lamb and Hoke, 1997).

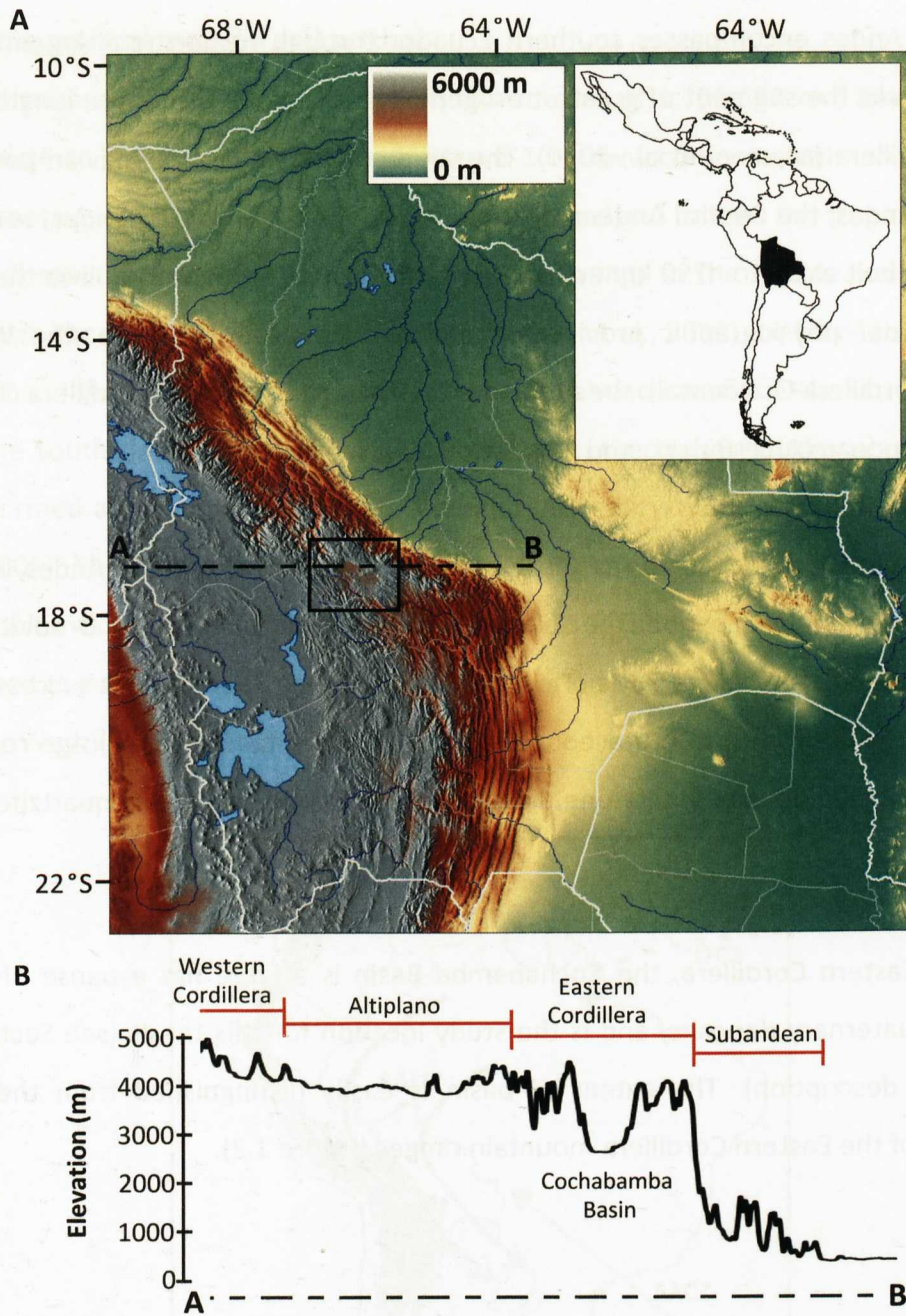


**Figure 1.1** Extent of the Tropical Andes biodiversity hotspot within South America and the major atmospheric features of the climate system. ITCZ = Intertropical Convergence Zone, SALLJ = South American Low Level Jet, SACZ = South Atlantic Convergence Zone. Data sourced from Mittermeier et al. (2004) and Sylvestre (2009).

The Central Andes encompasses southern Ecuador through to northern Argentina and Chile and marks the segment of greatest orogenic volume along the entire length of the Andean Cordillera (Mamani et al., 2010). The southern Peruvian and Bolivian portion of the Central Andes, the Central Andean orocline ( $\sim 13^{\circ}\text{S}$ – $28^{\circ}\text{S}$ ), forms the widest section of the orogenic belt at up to  $\sim 750$  km across (Graham, 2009). Throughout Bolivia the Andes consists of four physiographic provinces, from west to east these are: the Western Cordillera (Cordillera Occidental), the Altiplano, the Eastern Cordillera (Cordillera Oriental) and the Subandean (Arce-Burgoa and Goldfarb, 2009; see Figure 1.2).

The Eastern Cordillera, which forms the back-arc region of the Bolivian Andes, reaches greater than 5000 m in elevation. The Eastern Cordillera mainly consists of Ordovician age geological material, 488.3–443.7 Ma (Tawackoli et al., 1996). More recent successions of Devonian (416–359 Ma) and Cretaceous through Neogene (145–2.5 Ma) age rocks are also present, including; shale, siltstone, limestone, sandstone, slate, and quartzite (Arce-Burgoa, 2009).

Within the Eastern Cordillera, the Cochabamba Basin is a large flat expanse of fluvio-lacustrine Quaternary deposits, and is the study location for this thesis (see Section 1.4 for detailed description). The extent of basin is easily distinguished from the steep topography of the Eastern Cordillera mountain ranges (Figure 1.2).



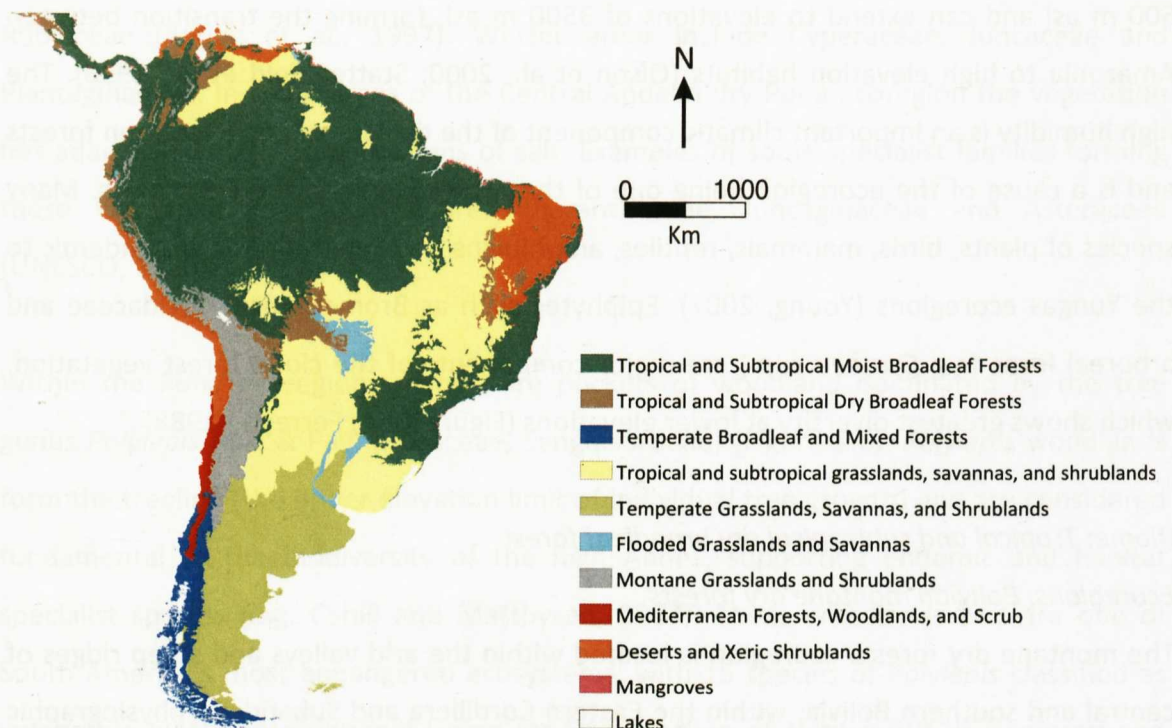
**Figure 1.2 A)** Digital shaded relief map (SRTM data; 90 m grid resolution) of Bolivia. **B)** Elevational cross-section of line A–B. Corresponding physiographic provinces and Cochabamba Basin, the study area for this thesis, is shown (black box).



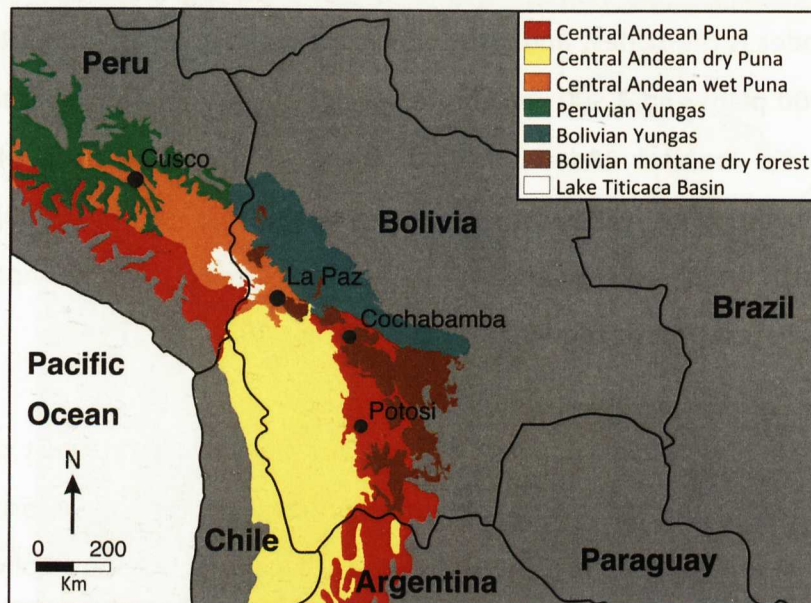
### 1.1.2) Modern ecology

The Tropical Andes is the richest and most biologically diverse region on earth (Killeen et al., 2007). 45,000 plant and 3,300 vertebrate species have been documented within the boundaries of the Tropical Andean hotspot, including 6.7% and 5.7% of the global endemism in plants and vertebrates respectively (Myers et al., 2000). The high biodiversity is attributable to the variety of habitats encompassed by the hotspot as well as its extremely heterogenetic topography (Foster et al., 1994).

Of all locations in the Tropical Andes, the eastern slopes, where moist air from the Amazon collides with the barrier of the Andean Cordillera, are the most biologically diverse (Killeen et al., 2007). In just the southern Peruvian and northern Bolivian sections of these eastern Andean slopes, 3 biomes (Figure 1.3) and 6 terrestrial ecoregions (Figure 1.4) have been recognised by the World Wide Fund for Nature (WWF). These ecological divisions are defined by their geographically distinct assemblages of species and communities, together with present day environmental conditions (Olson et al., 2001). These 6 ecoregions form 3 main groups; the Bolivian and Peruvian Yungas, Bolivian montane dry forests and the Central Andean Puna.



**Figure 1.3** South American biomes. As defined by the WWF (Olson et al., 2001).



**Figure 1.4** Ecoregions of the Bolivian and southern Peruvian Andes. As defined by the WWF (Olson et al., 2001).

*Biome: Tropical and subtropical moist broadleaf forest*

*Ecoregions: Bolivian and Peruvian Yungas*

The tropical moist cloud forests of the Bolivian and Peruvian Yungas ecoregion occur from 500 m asl and can extend to elevations of 3500 m asl, forming the transition between Amazonia to high elevation habitats (Olson et al., 2000; Stattersfield et al., 1998). The high humidity is an important climatic component of the deciduous and evergreen forests and is a cause of the ecoregion being one of the most diverse in the Neotropics. Many species of plants, birds, mammals, reptiles, amphibians and invertebrates are endemic to the Yungas ecoregions (Young, 2007). Epiphytes such as Bromeliaceae, Orchidaceae and arboreal ferns (e.g *Cyathea* spp.) are major components of the cloud forest vegetation, which shows greatest diversity at lower elevations (Figure 1.5A; Ferreyra, 1988) .

*Biome: Tropical and subtropical dry broadleaf forest*

*Ecoregions: Bolivian montane dry forests*

The montane dry forests ecoregion is located within the arid valleys and steep ridges of central and southern Bolivia, within the Eastern Cordillera and Subandean physiographic provinces of the Andes. The ecoregion marks the transition between the Yungas to the east, and the Puna to the west (Olson et al., 2000). The ecoregion vegetation is



characterised by dry, sparsely vegetated slopes with shrubs, dry forest, thornscrub and cactus formation. Important genera include *Acacia* and *Prosopis* (family Fabaceae), *Dodonea* (Sapindaceae) and *Schinopsis* (Anacardiaceae) and *Proustia* (Asteraceae) (Ergueta and de Morales, 1996).

*Biome: Montane grassland and shrubland*

*Ecoregions: Central Andean Puna*

Above the continuous montane forest line (also called timberline), uncultivated sections of the high Andes are principally grassland, commonly referred to as Puna (Figure 1.5B). The area encompasses elevations higher than ~3500 m asl. This includes snow-capped peaks, volcanoes, salt flats, high lakes, plateaus, mountain pastures and several rivers systems (Olson et al., 2000). Puna ecoregion vegetation consists primarily of grasslands made up of different grass (Poaceae) species, primarily the genera *Calamagrostis*, *Agrostis* and *Festuca*. Within the the Central Andean Puna, two ecoregions are identified, the Central Andean wet Puna, and the Central Andean dry Puna. Additional important vegetation of the wet Puna includes the grass genera *Paspalum* and *Stipa*. Plants other than grasses that predominate include 12 genera of Asteraceae, and up to 3 genera of Brassicaceae, Campanulaceae, Caryophyllaceae, Rosaceae, Scrophulariaceae and Rubiaceae (Young et al., 1997). Wetter areas include Cyperaceae, Juncaceae and Plantaginaceae. In some areas of the Central Andean dry Puna ecoregion the vegetation has adapted to high concentrations of salt. Examples of some specialist families forming these halophyte communities are Amaranthaceae, Juncaginaceae and Asteraceae (UNESCO, 1980).

Within the Puna ecoregions matrix, are pockets of woodland dominated by the tree genus *Polylepis* Ruiz & Pav. (Rosaceae, Sanguisorbeae) (Figure 1.6). *Polylepis* woodlands form the treeline (the upper elevation limit of individual tree growth) and are considered fundamental to the biodiversity of the high Andes, supporting endemic and habitat specialist species (e.g. Cahill and Matthysen, 2007). These woodlands and are one of South America's most endangered ecosystems, with 15 species of *Polylepis* classified as vulnerable by the International Union for Conservation of Nature (IUCN) (Jameson and Ramsay, 2007; Navarro et al., 2005).



**Figure 1.5** Two of the main ecoregions of the Bolivian and Southern Peruvian Tropical Andean hotspot.

**A)** Yungas cloud forest. **B)** Central Andean Puna. Photograph A is provided by William Gosling.

Taxonomically complex, the earliest estimate of the number of *Polylepis* species was made using herbarium specimens (Bitter, 1911), and concluded that 33 were known with an additional 9 subspecies and 18 varieties. Since this pioneering work, subsequent taxonomic refinement following field collection by Simpson (1979), led the number of species to initially drop to 15, but subsequently this has steadily risen (Kessler and Schmidt-Lebuhn, 2006). The most recent study recognised 26 species across the continent (Table 1.1), but the authors note that 2 additional Peruvian populations may merit species rank if more supporting evidence (herbarium and field material) is located to adequately confirm their status (Kessler and Schmidt-Lebuhn, 2006). The genus has its centre of diversity and highest endemism in an area ranging from central Peru to southern Bolivia (Navarro et al., 2005: Table 1.1).

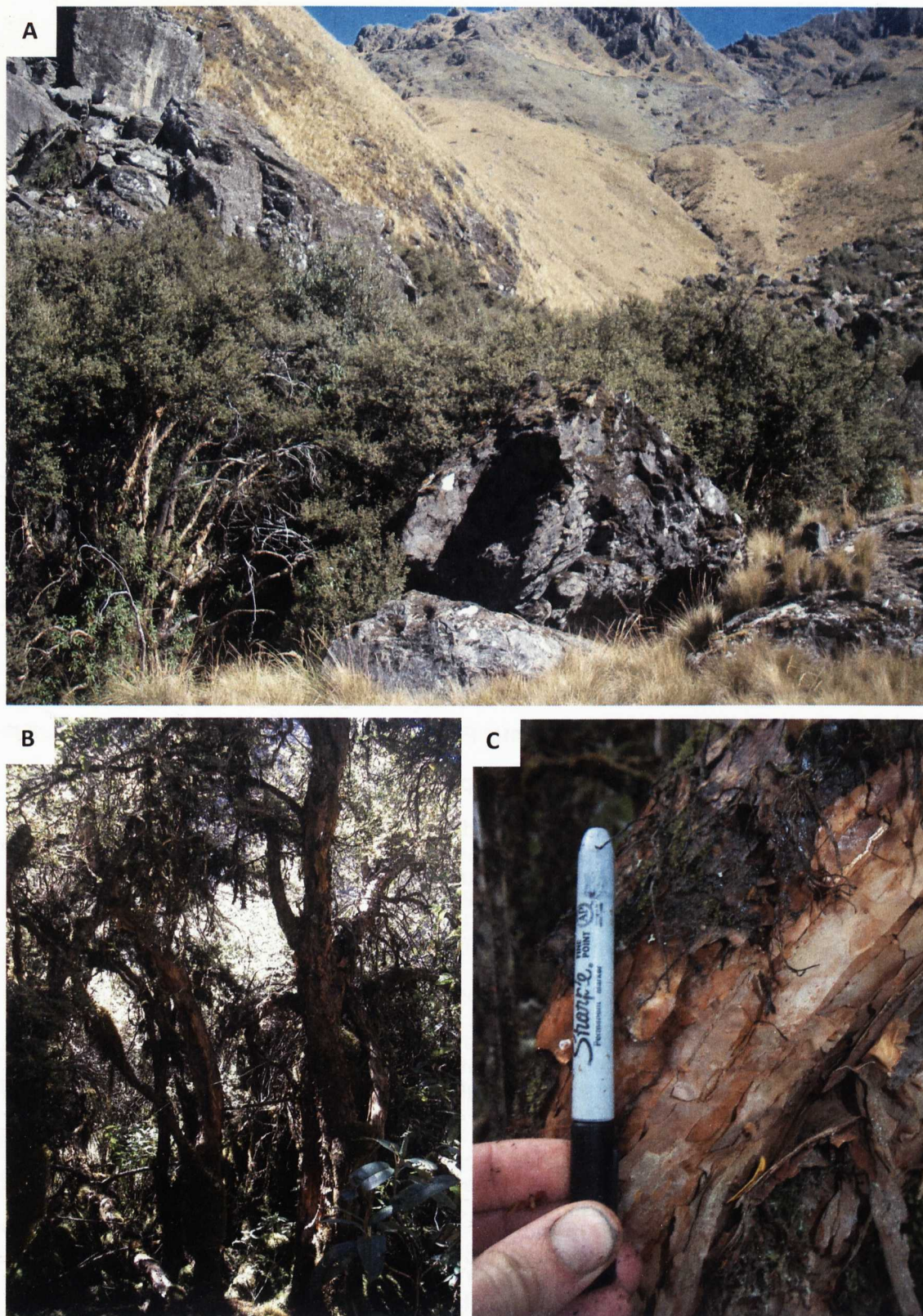
Country	Species Richness (Endemism)
Venezuela	1
Colombia	3 (1)
Ecuador	7 (2)
Peru	14 (3)
Bolivia	13 (4)
Chile	2
Argentina	4 (1)

**Table 1.1** The distribution of *Polylepis* species across South America (north – south). Data from Kessler and Schmidt-Lebuhn (2006). Total and endemic special numbers shown.

*Polylepis* is one of only two arborescent genera that grow at elevations of up to almost 5000 m asl. The highest tree species found in the Northern Hemisphere, *Juniperus tibetica* Kom, has been documented in a stand at 4900 m asl in Tibet (Miehe et al., 2007). In comparison, adaptive radiation of the genus *Polylepis*, led its colonisation of higher and more arid environments, and today it can surpass 5000 m asl (Kessler, 2002; Navarro et al., 2005). This survival is due to several adaptations of *Polylepis*: i) increased frost resistance (Graf, 1981), ii) an ability to alter nutrient uptake in cold conditions (Hertel et al., 2008), and iii) to survive the damaging effects of increased UV-radiation at high elevation (González et al., 2007).

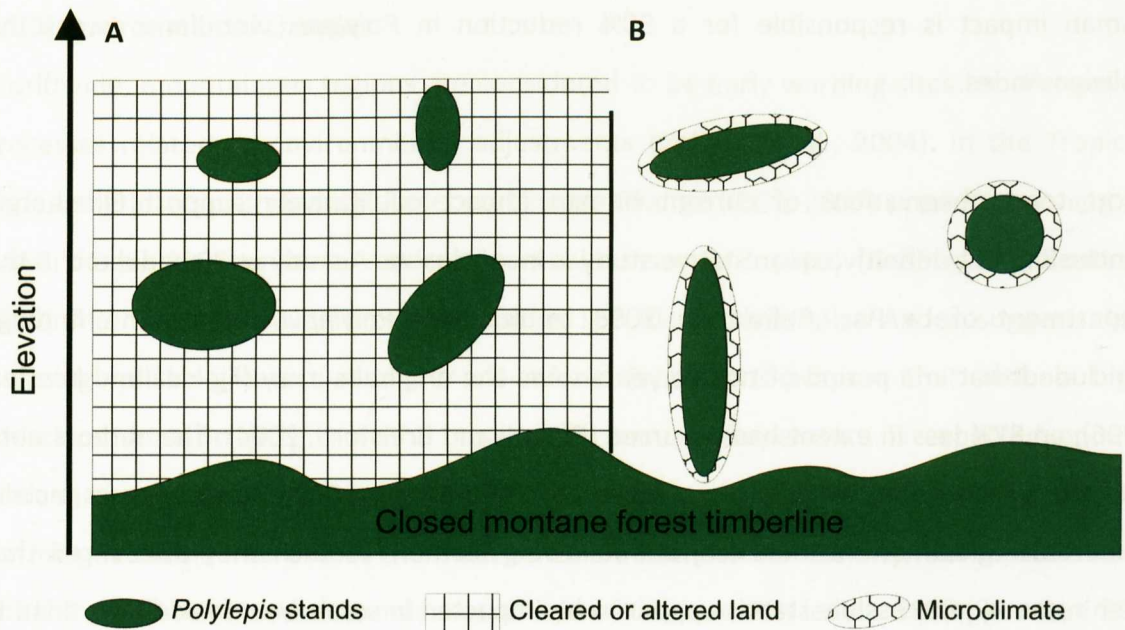
Although, the high altitude survival and adaptations of *Polylepis* still warrant discussion, it is the fragmented network of *Polylepis* growth above the continuous treeline (Figure 1.7), and the enclaves of high biodiversity they support, that have attracted the attention of conservationists and ecologists (Gosling et al., 2009). The cause of the woodland patches or stands is a question scientists have struggled to interpret and the ongoing discussion of these forest islands in South America led Miehe and Miehe (1994) to name the debate the “*Polylepis* Problem”, which was further discussed by Kessler (2002a).





**Figure 1.6** *Polylepis* woodlands of Cochabamba, Bolivia. **A)** Typical setting of modern *Polylepis* woodland stands within a boulder field. **B)** Dense growth structure and understory vegetation of *Polylepis*. **C)** Distinctive papery bark of *Polylepis* branches, a frost resistant adaptation. Photographs A and B provided by William Gosling.





**Figure 1.7** Schematic representation of the potential causes of *Polylepis* fragmentation. **A)** Anthropogenic fragmentation caused by clearance of woodland. **B)** Natural fragmentation caused by microclimates. In both scenarios, a very similar woodland structure can be created, and unless obvious local forcing factors are apparent, distinguishing the relative impact of drivers can be difficult. Based upon a drawing of Körner and Paulsen (2004) of mountain vegetation types.

Early explanations of the patchy distribution were based upon the idea that naturally occurring features in the landscape created unique microclimates. These allow for locally favourable conditions of air temperature and/or moisture content of the soils, and thus support tree growth above the closed timberline of the montane forests (Figure 1.7B; Fjeldså and Kessler, 1996). Apparent favourable conditions were located amongst boulder fields or rock falls (e.g. Figure 1.6A), and within steep sided valleys or ravines.

A challenge to the original view of natural factors governing the *Polylepis* distribution was put forward by Ellenberg (1958), who argued that the current state of the forests was due primarily to a long history of human activity which removed large areas of the woodland leaving only isolated patches. This hypothesis was later built upon by the work of Kessler (1995) and Wille et al (2002). Fundamentally, Ellenberg argued that *Polylepis* was the natural climax forest of the high Andean regions without human interference. Since this suggestion, climate niche reconstructions based on present-day distribution, has allowed estimations of past *Polylepis* cover. From this, Fjeldså and Kessler (1996) estimate that

human impact is responsible for a 90% reduction in *Polylepis* woodland across the Bolivian Andes.

Short term observations of current human impact qualitatively support Ellenberg's conclusion, but definitive quantitative study is inconclusive. A study was conducted in the Department of La Paz, Bolivia, in 2003 to resurvey *Polylepis* extent. The findings concluded that in a period of twelve years since the original survey (Fjeldså and Kessler, 1996), an 87% loss in extent had occurred (Purcell and Brelsford, 2004). The authors note that the sites studied were easily accessed by road and thus may have been especially vulnerable to human interference, but following further research they discovered that even remote, inaccessible stands appear to be impacted in some way. In addition, a study of air photographs over a 50-year period showed a "significant" decline in canopy density in 10% of forest patches, from Cordillera de Vilcanota, Peru (Jameson and Ramsay, 2007).

However, despite these survey results, it remains unclear to what degree and extent the Andean *Polylepis* woodlands have been impacted by human activity across the region, and if the woodland patches are also being formed or altered by changing environmental conditions, and/or the creation of unique microclimates. Indeed, Fjeldså (2002) reports two photographic studies from Peru, one over a period of >60 years, that both show minimal or no change in the abundance of *Polylepis* woodlands (Byers, 2000).

Fuelling the "*Polylepis* Problem" debate is the uncertainty that remains regarding the natural extent to which *Polylepis* woodland would cover the land if there was no human interference, and whether or not the current stands are remnants of a formerly much more extensive vegetation zone.

### 1.1.3) Environmental changes

Worldwide, mountainous regions are considered to be early warning sites for changes in processes related to environmental adjustments (Ørbæk et al., 2004). In the Tropical Andes, the Intergovernmental Panel on Climate Change (IPCC, 2007) predicts warming of 2.5–3.5°C by 2100 under a moderate emissions scenario (A1B) (Gosling and Bunting, 2008). Alarming however, modelling studies specific to the Tropical Andes, suggests that warming will be greatest at higher elevations. Predictions propose that under a high emissions scenario (A2), a 4–5°C increase in annual temperature is expected on the eastern slopes above 3500 m asl by 2100 (Urrutia and Vuille, 2009). Globally, climate warming is considered one of the most serious threats to biodiversity. Using predictions of habit distribution and size under a scenario of doubled CO<sub>2</sub> levels, 3000 plant and 200 vertebrate species are estimated to become extinct in the Tropical Andes alone as a result of climatic warming (Malcolm et al., 2006).

#### *Modern climate*

Climate, particularly precipitation, in the Tropical Andes is associated with a number of major atmospheric features (Figure 1.1). Seasonally this area is dominated by the South American Summer Monsoon (SASM; Zhou and Lau, 1998), which is in broad association with movement of the Intertropical Convergence Zone (ITCZ), variability of the South American Low Level Jet (SALLJ; Vera et al., 2006) and the South Atlantic Convergence Zone (SACZ; Sylvestre, 2009). Over inter-annual, decadal and longer timescales, adjustments in the El Niño-Southern Oscillation (ENSO) are considered to be the largest source of climate variation (Chiang, 2009; Philander, 1990).

In the Bolivian Andes the most striking evidence of a changing climate is presented by glacier retreat, and today, the Zongo, Chacaltaya, and Charquini Sur glaciers are shrinking in area and volume (Francou et al., 2005). The Chacaltaya glacier, previously the site of the World's highest ski field, lost 90% of its area in the 13 years before 2005, with total loss expected soon after 2010 (Berger et al., 2005). As well as changes in precipitation, the cause of this regional retreat is due to a warming troposphere (Francou et al., 2003), which is particularly concerning considering the upper and middle parts of this atmospheric layer are expected to experience the greatest heating in the future (Urrutia and Vuille, 2009). Although detailed, these records rely on direct measurements, and as

such only extend back c. 70 years. These records include the analysis of historic photographs, exploration notes and cultural references. However, to fully understand how changing climates, both rapid and gradual, have influenced the vulnerable ecosystems of the Tropical Andes, longer-term data sets are required. Knowledge of past ecosystem response to climate change, including information about the rate and duration of changes, enables scientists to predict and understand the possible responses to anticipated warming in the future.

### *Past climate*

Records of past climatic changes driven by orbital cycles have been available for more than 30 years. These include records from ice cores (e.g. Greenland; Camp Century, GRIP, NorthGRIP (Johnsen et al., 2001), Antarctica; Vostok, EPICA (EPICA Community Members, 2004; Jouzel et al., 1987)), and marine sediment records (e.g. the Deep Sea Drilling Project and the Integrated Ocean Drilling Program (Bond et al., 1993; Herbert and D'Hondt, 1990). Today, several long-term records of climatic change are also available from the Andean mountain range from predominantly lake and ice cores (see Section 1.2). Although there is some asynchrony between hemispheres in the timing of both glacial-interglacial transitions and abrupt events (Lynch-Stieglitz, 2004; Vandergoes et al., 2005), in general there is a global pattern of climate change.

In the Central Andes, the climate of the Last Glacial Maximum (LGM;  $21 \pm 2$  ka BP; Mix et al., 2001) has been characterised as being  $\sim 7\text{--}8^\circ\text{C}$  colder than modern climate (on the Altiplano) with regionally variable changes in moisture availability (Baker et al., 2003; Cook, 2009; Sylvestre, 2009). The subsequent deglaciation and the Holocene (c. 11.7 ka BP–present) is now understood as a time of fluctuating moisture availability, with some small-scale variation in temperature (Bush et al., 2005). Although the timings, impacts and mechanisms driving environmental change during this period are still debated, the response of environmental systems to key global events have now been recognised, including; a Bølling/Allerød type warming (c. 15–14.0 ka BP), a Younger Dryas type cold event (c. 12.9–11.6 ka BP), and the mid-Holocene dry event (MHDE; c. 8–5 ka BP; Rasmussen et al., 2006; Sandweiss et al., 1996; Thompson et al., 1998; Urrego et al., 2009; Zech et al., 2010). In addition, adjustments in climate systems such as the El Niño–Southern Oscillation (ENSO), the South American summer monsoon (SASM), and the



Intertropical Convergence Zone (ITCZ) have also been observed in the palaeorecords (e.g. Bräuning, 2009; Moy et al., 2002; Vuille and Werner, 2005).

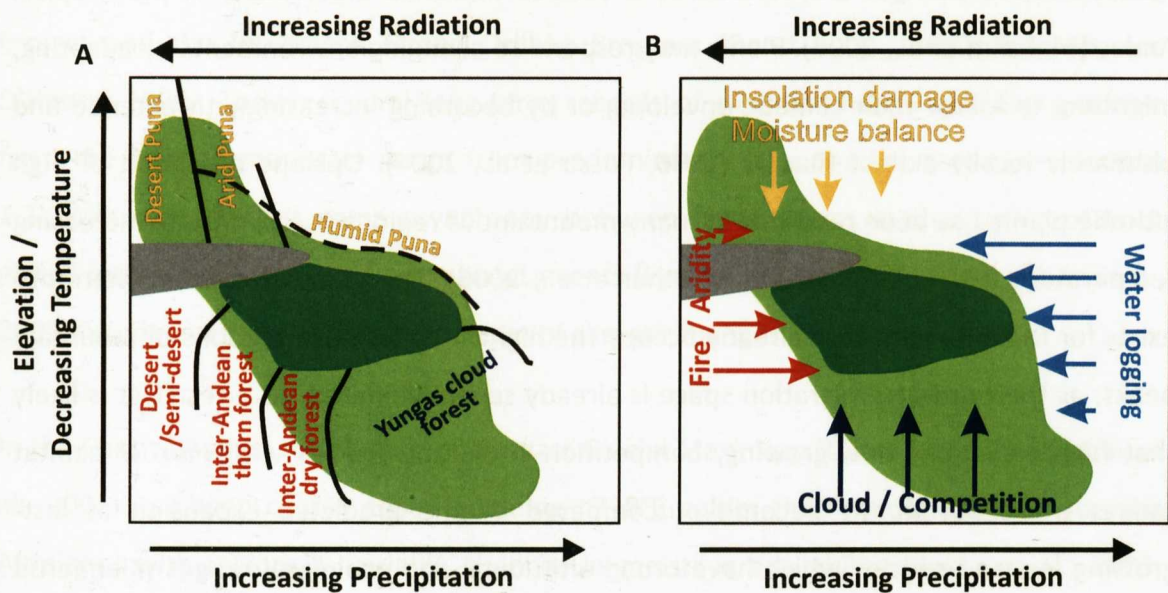
With an increase in the number of records available, it has become apparent that the impact, scale and nature of climate events has been spatially non-uniform across the Tropical Andes. Local factors, included human occupation, often disguise regional patterns. In addition, the distribution of study locations is unevenly spread across the Tropical Andes and so many regions that are climatically sensitive today remain unexplored in the palaeoclimate context and thus unrepresented in regional scale studies.

#### *Climate impacts on ecology*

Future climate changes are considered a serious threat to biodiversity in the Tropical Andes (Malcolm et al., 2006). Plants may respond to changing environments by adapting, migrating to follow their climatic envelope, or by becoming increasingly threatened and ultimately locally extinct (Bazzaz, 1996; Fossa et al., 2004). Upslope migration of high altitude plants has been recorded in many mountainous regions in response to increasing temperature (Lenoir et al., 2008; Walther et al., 2005). The greatest concern therefore exists for those species that already occupy the highest colonisable sections of mountain peaks, as their upward migration space is already severely limited. As a result, it is likely that high elevation, slow-growing, competition-intolerant species with narrow habitat ranges will subsequently become outcompeted by the predicted expansion of fast-growing lowland species which have broad altitudinal and ecological ranges (Klanderud and Birks, 2003). However, in the Andes, where future precipitation changes are believed to be spatially much less coherent and unpredictable (Urrutia and Vuille, 2009), the likely response of vegetation to these future changes is much less understood. Furthermore, in these Andean environments the usual concepts of upslope vegetation migration in response to temperature increase are complicated by nonlinear changes and complex feedback mechanisms (Bush et al., 2010).

Although future climate changes threaten the biodiversity, the past history of climatic fluctuation is likely to have had a major influence on the development and shaping of the Tropical Andes. Natural changes in climate could cause movement in the position of

ecological limits for species and communities, thus contracting or expanding suitable habitat ranges. Indeed, the natural ecological limits of *Polylepis* woodlands have been investigated and help to explain, in part, the boundaries with the Andean grassland matrix. Modified from the ideas put forward by Fjelds  and Kessler (1996), Gosling et al. (2009) further developed conceptual models of the environmental limitations upon *Polylepis* woodland under a variety of climate conditions (Figure 1.8). These models help the visualisation of the influence of the governing factors of moisture, temperature and insolation and how these are linked to the actual ecological limits of *Polylepis* woodland niche space. Unfortunately however, these ecological limits are frequently obscured during modern field recording studies by the often un-measurable impact of recent human activities.



**Figure 1.8** Natural limits of *Polylepis* in Bolivia under modern conditions. **A)** Distribution of woodland amongst other vegetation types. **B)** Conceptual model of limiting factors. *Polylepis* niche space = dark green, *Polylepis* potential niche space = light green, Altiplano zone = grey. Redrawn from Gosling et al. (2009) and based on the original schematic of Fjelds  and Kessler (1996).

#### 1.1.4) Human occupation

Although human populations have existed in the South American Andes since the late Pleistocene, debate still continues on whether their arrival was before or after the start of the Holocene (11.7 ka BP) (Coltorti et al., 2010; Dillehay, 1999; 2000; 2008; Lavall e,

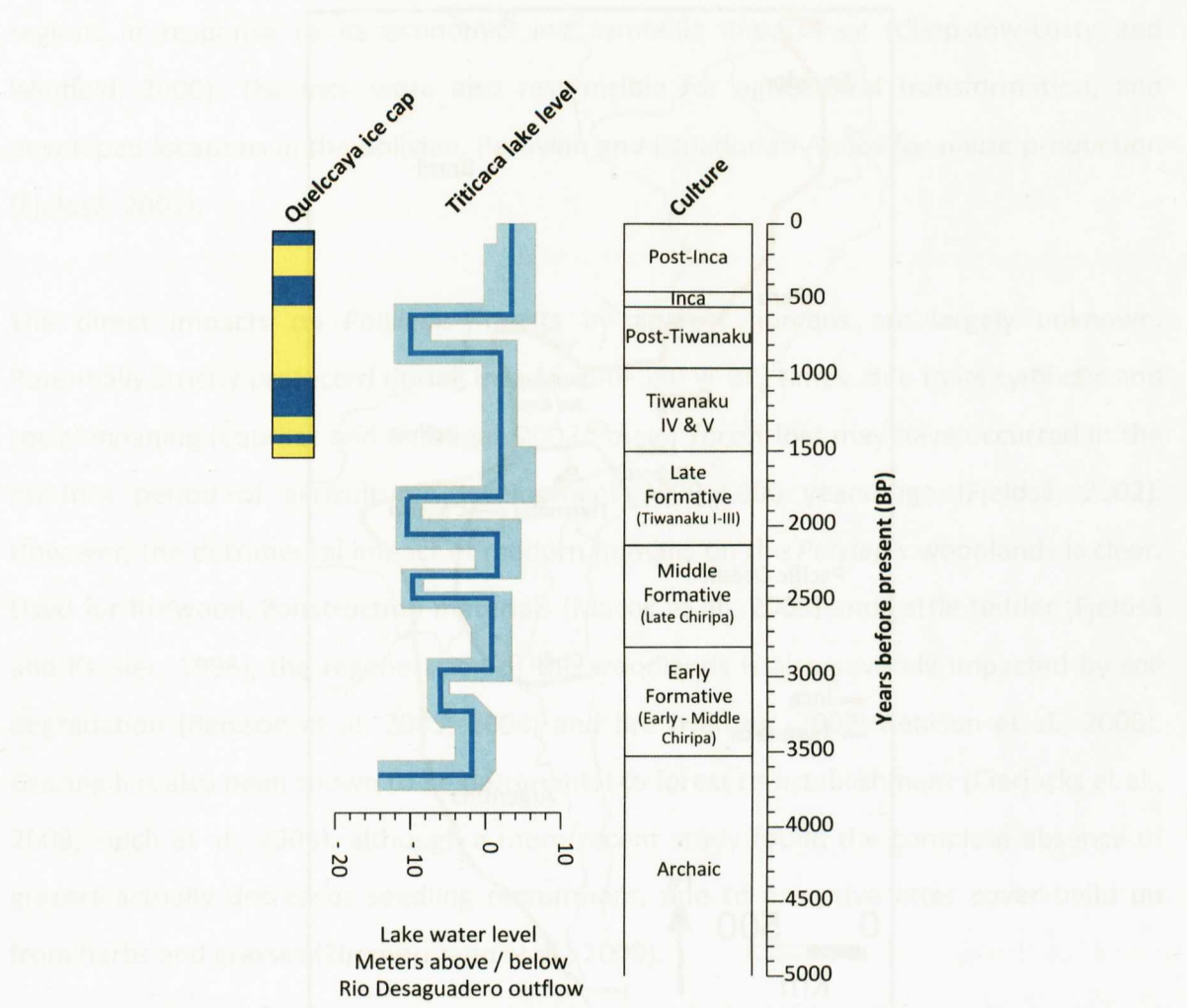
2000; Lynch, 1990; Roosevelt et al., 1996). The extent of the environmental impact caused by humans is also unresolved. Some authors consider that fire may have been utilised as a hunting aid from the arrival time of humans (Ellenberg, 1979), while others consider early hunter-gatherer based exploitation to be opportunistic with minimal environmental impact (Mondini, 2002). Evidence that fire has been a natural component of central Andean ecosystems long before the arrival of humans (Gosling et al., 2009), adds complexity to the debate as differentiating a human vs. natural signal is required. What is clear however, is that reliance on local, seasonal (plants) and/or mobile (animal) resources led early human populations to utilise the terrain and the ecological diversity of the Andean mountains and the Amazon basin, and tracked changes in biota driven by the climatic shifts (Dillehay, 2008). Increasingly evident, is that by the early Holocene (c. 9 ka BP), dependence on resources had increased, and people began to alter the natural habitats by persistent hunting, transportation of plants, and the deliberate or accidental burning of the landscape (Dillehay, 2008).

Compared to other areas of the Andes, very little is known about prehistoric populations in Bolivia, and few occupation markers have been discovered (Aldenderfer, 2009). While this is potentially an artefact of archaeology, it is also likely that it reflects reality and is indicative of very low population densities and perhaps an inability to exploit difficult environments (Dillehay, 2008). Kolata (1993), speculated that the first humans reached Lake Titicaca, on the Altiplano border of modern Peru and Bolivia, around 14,000 years ago, although a greater consensus suggests that humans did not reach the region until 1000 years later (Dillehay, 2000; Lavallée, 2000). By 10,000 years ago, seasonally nomadic populations in the inter-Andean valleys interacted with other such groups centred on the Altiplano (around Lake Titicaca) and Pacific coast, and presumably, those of the Amazonian Basin (Kolata, 1993).

Across much of the Andes, including Bolivia, the middle-Holocene period (c. 9–3 ka BP), suffered what has been disputably labelled as times of “archaeological silence” (Grosjean et al., 1997). Although variable in the north-south timings (Sandweiss and Richardson, 2008), it is linked to the mid-Holocene dry event (8–5 ka BP) identified from many Andean locations (e.g. Hillyer et al., 2009; Paduano et al., 2003; Urrego et al., 2010; Valencia et al.,

2010). During this time very little evidence of human population exists for the region, even from Lake Titicaca, one of the heartlands of dominant pre-Columbian populations. However, until about 6000–4000 years ago, populations around the Titicaca Lake basin, remained hunter-gatherers (Kolata, 1993; Young-Sanchez, 2004). By 6000 years ago foraging, hunting, fishing, and birding had all become valuable and well developed subsistence strategies (Hastorf, 2008). This cultural style most likely also represents the general situation across Bolivia at this time. By c. 3500 years ago, farming began in the fields surrounding Lake Titicaca (Kolata, 1996). It is likely this agricultural development was in response to the increasing water levels of Lake Titicaca (Abbott et al., 1997) (see Figure 1.9). The middle stages of the Holocene saw the widespread utilization of fire and, in many locations, expansion of agricultural development.

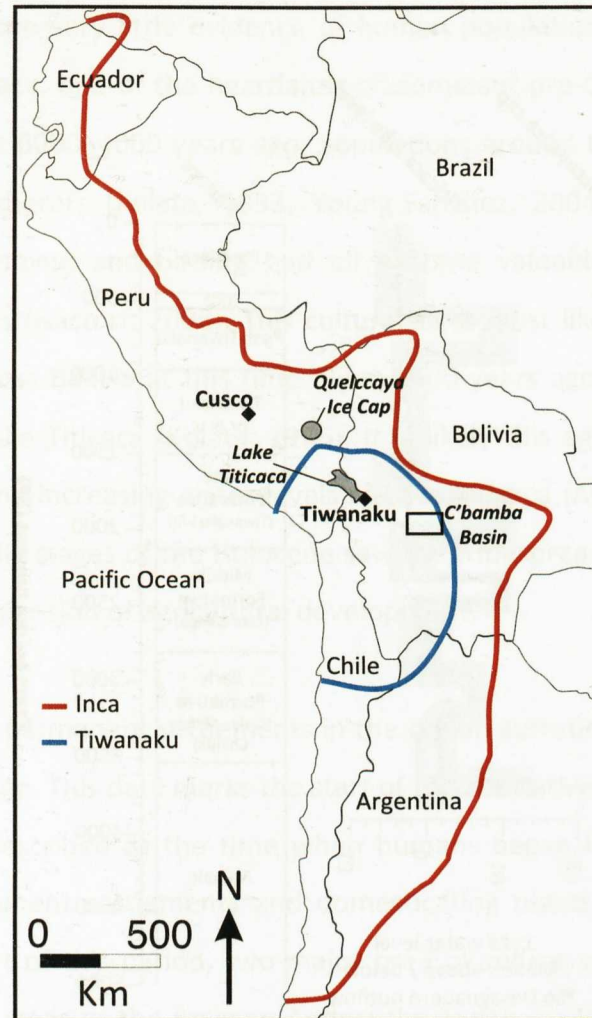
The first evidence of permanent settlements in the region surrounding the Titicaca Basin starts c. 3500 years ago. This date marks the start of the Formative Period or Initial Period (Figure 1.9) and is described as the time when humans began marking the landscape, creating more permanent settlements and domesticating plants and animals (Hastorf, 2008). Since the start of this period, two major pre-Columbian societies or polities had influence over large areas of the Bolivian Andes: the Tiwanaku (c. 1500–900 yr BP) and the Inca (c. 650–550 yr BP) (Figure 1.10). During these times, it is generally agreed that central Andean civilised cultures first evolved as city-like constructions appear (Isbell, 2008).



**Figure 1.9** Basic cultural chronology and inferred climatic conditions of the Bolivian Altiplano. Dust levels from the Quelccaya ice core record (Thompson et al., 1985). Yellow = dryer, Blue = Wetter. Lake Titicaca water levels (Abbott et al., 1997). Blue shaded area represents range of uncertainty.. Cultures based on the chronologies of Bandy (2004), Isbell (2008) and Janusek (2008).

The collapse of the Tiwanaku state, around 900–1000 years before present (yr BP), has been linked to a prolonged drought around Lake Titicaca, as indicated by low lake levels (Abbott et al., 1997; Binford et al., 1997), and an elevated dust signal from the nearby Quelccaya (Peru) ice core record (Figure 1.9 and 1.10; Thompson et al., 1985). The subsequent transitions from Tiwanaku fragmentation and collapse, Inca Empire rule and violent Spanish conquest (c. 550 yr BP) is certain to have had major impacts on both societies and the landscapes they occupied.





**Figure 1.10** The territorial spheres of the Inca and Tiwanaku. The locations of important pre-Columbian cities, palaeo records discussed, and the Cochabamba Basin (location of this study) marked. Territorial extents from Silverman and Isbell (2008).

### *Human impacts on ecology*

Ancient human impacts on the biodiversity of the Tropical Andes, are often difficult to detect and interpret. Overall, impacts can be linked to five main features: settlement and monument building, agricultural development, irrigation, domestication of animals and the use of fire. Today, much of our information has been gained from macroscopic and microscopic sediment charcoal analysis, but the cause of fire can be both natural and human driven. Besides the use of fire, camelid pastoralism and caravans were also hugely important for pre-Columbian peoples (Lynch, 1983), and there is now good evidence to suggest that raised bed agriculture around Lake Titicaca was occurring before c. 2400 years ago (Kolata, 1996). Later, *Alnus* agroforestry by the Inca has been identified in other

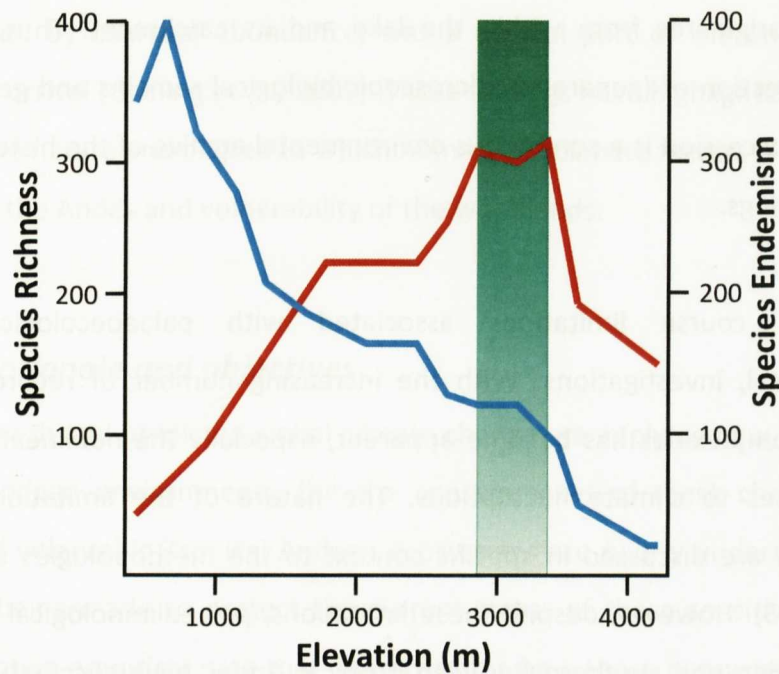
regions in response to its economic and symbolic importance (Chepstow-Lusty and Winfield, 2000). The Inca were also responsible for agricultural transformation, and developed locations in the Bolivian, Peruvian and Ecuadorian Andes for maize production (Fjeldså, 2007).

The direct impacts on *Polylepis* forests by ancient humans are largely unknown. Potentially strictly protected during Inca (c. 650–550 yr BP) times, due to its symbolic and social meaning (Capriles and Bedregal, 2002), major forest loss may have occurred in the pre-Inca period of agricultural development 3000–5000 years ago (Fjeldså, 2002). However, the detrimental impact of modern humans on the *Polylepis* woodlands is clear. Used for firewood, construction materials (Macek et al., 2009) and cattle fodder (Fjeldså and Kessler, 1996), the regeneration of the woodlands is also severely impacted by soil degradation (Renison et al. 2005; 2004) and fire (Hensen, 2002; Renison et al., 2006). Grazing has also been shown to be detrimental to forest re-establishment (Cierjacks et al., 2008; Teich et al., 2005), although a more recent study found the complete absence of grazers actually decreases seedling recruitment, due to excessive litter cover build up from herbs and grasses (Zimmermann et al., 2009).

Regardless of the reasons why *Polylepis* woodlands are at present reduced to enclaves of greater or lesser extent, the biodiversity they support, together with their social and economic importance, marks them as an unique habitat that clearly warrants our attention (Fjeldså and Kessler, 1996). Conservation and securing their survival is especially important when one considers that the much of the unique flora and fauna, including endemic species of birds, mammals and amphibians is perhaps a result of the long-term presence of the woodlands (Fjeldså and Kessler, 1996; Young, 2007). However, to assess and develop an effective policy to conserve and manage any ecosystem, including *Polylepis* woodlands, a robust understanding of the region's natural history through periods of varying stress levels is fundamentally required (Godwin, 1956; Willis et al., 2010; Willis and Birks, 2006).

Land managers in the high Bolivian Andes are currently encouraged to emphasize the use of *Polylepis* for the control of erosion and for the provision of firewood (Fjeldså and Kessler, 1996). This is due to its presumed former extent and high elevation ecological tolerance (Gosling et al., 2009) and the ability of *Polylepis* to thrive under a variety of modern climate and soil types (Ellenberg, 1979). One such project, the Asociación Ecosistemas Andinos (ECOAN), initiated the planting of 60,000 *Polylepis racemosa* trees, in a direct attempt to join up fragments of existing woodland (Aucca and Ramsay, 2005). While this extensive use of native tree species over exotic species holds many advantages, including for biodiversity conservation (Fjeldså and Kessler, 1996), without a record of the natural history of these high Andean ecosystems, we rely on speculative information about the natural woodland/grassland structure in order to guide our conservation approaches. Specifically to the ECOAN planting project, there is at present no consensus on whether the *Polylepis* woodland was continuous laterally in the Andean grasslands, and linking up modern day patches may actually be detrimental to the overall biodiversity of the Andes. Indeed, it has been shown that species endemism is highest at woodland patches and not in the continuous forest (Figure 1.11; Fjeldså and Irestedt, 2009). The type of long-term, baseline status data that is vital to inform conservation policy (Willis and Birks, 2006), can only be provided by palaeoenvironmental studies, and well designed palynology projects are vital in assessing at least some parts of the *Polylepis* problem (Bader, 2007; Kessler, 2002).





**Figure 1.11** Bird species richness and endemism along an elevational transect in the Carrasco National Park, Cochabamba, Bolivia. Green shading = zones with patchy arboreal vegetation, Blue line = species richness (number), Red line = mean species endemism (average inverse range size per species). While species richness shows a gradual decline with elevation, endemism peaks in woodland patches. Redrawn from (Fjelds  and Irestedt, 2009) using survey data and interpolations for missing sampling points.

## 1.2) Palaeoecology: tracing human and climate ecosystem impacts

In response to the demand for a long-term “natural” ecosystem baseline, records of climatic changes and/or holistic ecosystem adjustments have been examined in many parts of the Tropical Andean mountain range. From Bolivia and southern Peru, information has been sourced from ice cores (e.g. Thompson et al., 1998); lake sediments (e.g. Baker et al., 2001); and tree rings (e.g. Argollo et al., 2006). In addition, recent achievements in dating glacial moraines has successfully allowed the timings of ice expansion and retreat to be mapped in a broad range of locations (e.g. Blard et al., 2009; Rabatel et al., 2008; Smith and Rodbell, 2010; Zech et al., 2007; 2009).

Of all record types, lake sediments have been the most successful for Andean palaeoenvironmental reconstruction. From the time of formation, lakes almost always accumulate sediments continually, and are usually only halted during times of aridity when desiccation and sediment loss can occur if the lake dries out completely. Lake sediments comprise a mixture of biological remains and non-biological material which

predominately originates from within the lake and its catchment. Thus, with careful analysis of a selection of (generally) microscopic biological remains and geochemistry, a lake sediment succession is a continuous environmental archive of the history of the lake and its surroundings.

There are of course limitations associated with palaeoecological, including palaeolimnological, investigations. With the increasing number of records, a growing awareness of complexities has become apparent, especially the nonlinear responses of proxies and lakes to climate fluctuations. The nature of the limitations specific to palaeolimnology are discussed in specific context to the methodologies utilised in this thesis (Chapter 3). However, despite these limitations, palaeolimnological investigations across the Bolivian and southern Peruvian Tropical Andes have successfully started to provided the baseline environmental (e.g. Abbott et al., 2003), ecological (e.g. Urrego et al., 2010) and human impact (e.g. Paduano et al., 2003) data required in order to improve understanding of past landscape changes.

To obtain an understanding of past Andean woodland distribution from the fossil pollen record it is necessary to consider pollination mechanism and dispersal. Although anemophilous (wind pollinated), *Polylepis* does not produce much pollen (Chepstow-Lusty et al., 2005; Fjelds , 2002), and the pollen is not transport far from the parent tree (Salgado-Labouriau et al., 1977) and so its presence in a fossil record indicates a local, site-specific abundance. This, combined with many previous fossil pollen studies being conducted outside *Polylepis* diverse and dominant areas, means that detection in many records is poor. Therefore, any investigation that attempts to examine the natural history of the *Polylepis* woodlands needs to be careful considered and planned for that purpose, not appended to a project designed to investigate another research focus.

Thus far however, palaeo data is inconclusive in addressing the questions surrounding the *Polylepis* problem. Several studies of fossil pollen have highlighted the potential impact of humans on the woodland (Graf, 1979; Hansen et al., 1984). However, newer longer-term fossil pollen data from Lake Titicaca suggest that during previous interglacial periods, prior to human arrival in the catchment, *Polylepis* woodland cover fluctuated in response to climate (Hanselman et al., 2005; 2011). This sedimentary record has also revealed that

fire, ascertained by charcoal abundance, was a natural part of the environment long before human arrival (Gosling et al., 2009). These findings have highlighted the ambiguity surrounding the nature and degree to which human and climate factors ultimately govern the ecology of the Andes and vulnerability of the woodlands.

### ***1.3) Thesis rationale and objectives***

Population growth and predicted global climate change are applying new, and increasing, pressure to Andean environments, but the consequences of these changes upon the biodiverse and vulnerable Tropical Andean ecosystems are poorly understood. Although attempts are being made to protect the current status of these sensitive habitats, the only way to obtain empirical data that demonstrates how these ecosystems are likely to respond to future change, is to look to the past. The sensitivity of the Tropical Andean vegetation allows the evaluation and monitoring of change not only of modern, real-time observed adjustments but, crucially via the use of palaeolimnological investigation, of long-term shifts in species association to environmental changes in the past.

The period c. 21,000 yr BP, when the last major global climatic transition occurred (full glacial to interglacial conditions), and humans spread throughout South America, is a critical phase for understanding human and climate interactions. Within this time frame, the deglaciation period and early Holocene represents the most recent time when the ecosystems of the Tropical Andes were not substantially influenced by human practices, but were exposed to naturally varying ecological stress levels. The subsequent development of human culture through the Holocene lead to changes in resource use and practices, and placed the ecosystems they occupied under a unique set of pressures not previously experienced.

Because of the interrelated nature of human, vegetation, climate and fire (see Chapter 3), a knowledge of climate history is vital before we can fully understand the developments and impacts of early (and later) cultures (Dillehay, 2008; Sandweiss and Richardson, 2008). However, the palaeoenvironmental history of the Tropical Andes, as in much of the Neotropics, is still insufficiently understood and fragmentary due to a paucity and uneven spread of records, together with controversy in the interpretation of them. The

correlation of changing palaeoenvironments and human cultures, together with the scale of human-environment interactions, is an important issue that warrants continued discussion and debate. This is especially true if we are to fully understand the threats upon ecosystems today and how they may respond to changing environments in the future.

To address these knowledge gaps three specific research goals have been established for this thesis:

- i. To determine the scale and impact of climatic events, climate system adjustments and ecosystem responses in the Bolivian Andes since deglaciation, and to compare the uniformity and correlation of these changes with other Andean locations.
- ii. To determine how pre-Columbian population enclaves, distant from the civilization centres of Cusco and Tiwanaku, impacted the landscape that they occupied via the exploitation of agricultural development, domestication of animals and fire. To examine if these impacts were wholly detrimental to the biodiversity of the Tropical Andean region in which they existed.
- iii. To assess the drivers governing the current distribution of *Polylepis* woodland and Andean grassland, and determine if the historic growth patterns suggest a previous, more widespread dominance. To provide new data useful for conservation policies and management strategies to assist with the re-establishment of the natural ecosystem structure.

To address the research aims identified and the knowledge gaps outlined, there was a careful selection of study areas. Important to aid this selection is locating an area with: i) material suitable for the measurement of a variety of climate records that extend back to the deglacial period, ii) a high level of Tropical Andean biodiversity and vegetation sensitivity (e.g. *Polylepis* woodland), iii) a sensitivity to climatic change, and iv) a long history of human occupation. It is also important to locate an area understudied in the palaeo context, in order to provide the maximum amount of new information that can be then incorporated into the regional knowledge of environmental and human impacts of

Tropical Andean ecosystems. With these key requirements, the Cochabamba Basin in the Eastern Bolivian Cordillera was selected for investigation.

## **1.4) The Cochabamba Basin, Bolivia**

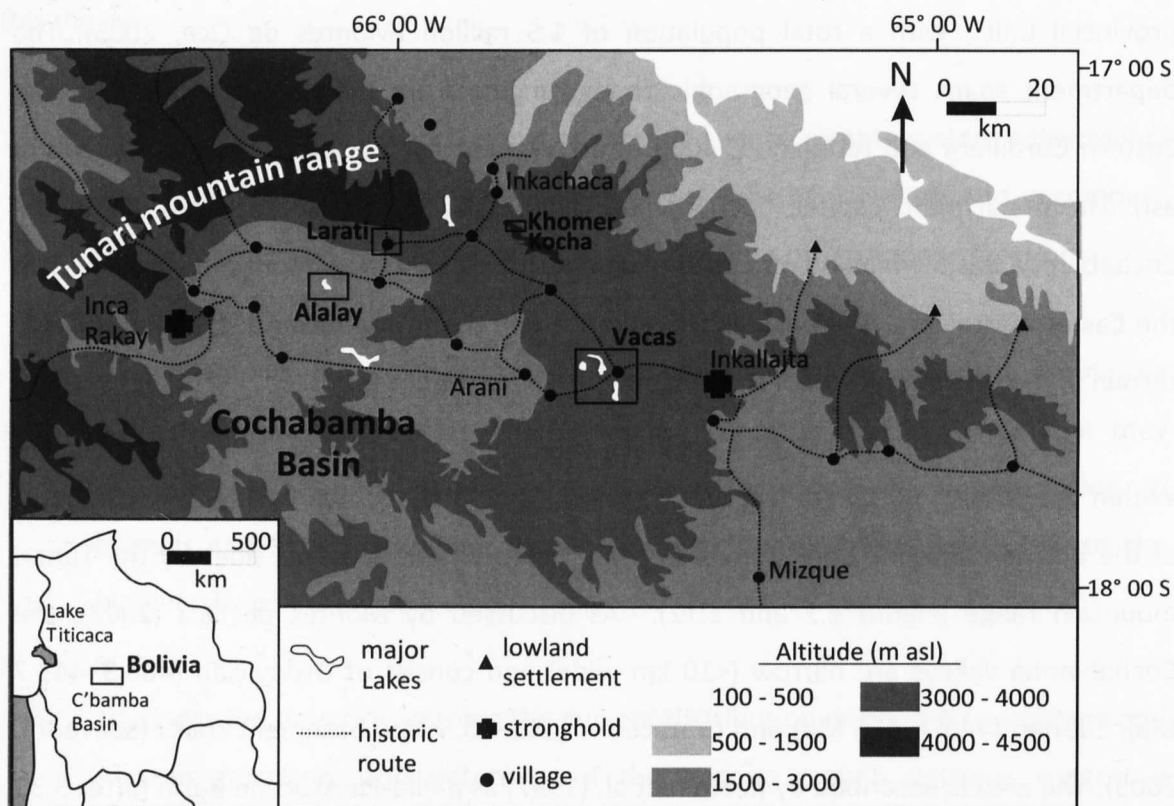
### **1.4.1) Geographical location and setting**

The department of Cochabamba covers an area of ~55,000 km<sup>2</sup> and is composed of 16 provincial units, with a total population of 1.5 million (Montes de Oca, 2005). The department spans several geographic zones ranging from the high mountains of the Eastern Cordillera and Altiplano (>4000 m asl) through to the lowland regions (<200 m asl). The department capital, Cochabamba city, (17°40', 66°14', 2500 m asl) lies in the Cochabamba Basin which is composed of a series of inter-Andean montane valleys within the Eastern Cordillera. The basin is characterised by the pronounced depression and flat terrain in the central portion of the Eastern Cordillera (Figure 1.2).

Within the Eastern Cordillera (McQuarrie, 2002), the Cochabamba Basin lies in the heart of the Bolivian Orocline and is limited on the northern and western sides by the Tunari mountain range (Figure 1.2 and 1.12). As discussed by Montes de Oca (2002), the Cochabamba valleys are narrow (<10 km wide) and consist of Ordovician (488.3–443.7 Ma), Silurian (443.7–416 Ma) and Cretaceous (145–65.5 Ma) basement rocks (Saavedra, 2005). The area is described by Keenan et al. (1997) as a Plio-Pleistocene Basin (after 5.33 Ma) due to the large volumes of sedimentary material deposited during the Quaternary. These Quaternary deposits consist of lacustrine material which develops into fluvio-lacustrine and fluvial sediments in the upper sections (Saavedra, 2005). The Quaternary successions attest to the existence of large water bodies in the valleys of Cochabamba, a situation recognized in the origins of the city name from the native words “Cocha” and “Phampa”, meaning swampy or waterlogged plains (Montes de Oca, 2005).

Today remnants of this large water body exist within the Cochabamba Basin, and together with smaller lakes created by local glaciation features in the surrounding mountain ranges, the region provides the palaeolimnological records required to address the research aims discussed (Section 1.3). From within and surrounding the Cochabamba

Basin, 8 lakes from 4 locations were identified from satellite imagery and maps as potential sites for palaeoecological investigation (Figure 1.12 and Table 1.2). Investigation of the sites at Cochabamba city (Laguna Alalay), Sacaba (Laguna Larati and Caluyu), Vacas (Lakes Parkokocha, Acerokocha, Juntutuyo, Kollpakocha, Challacaba and Yanatama) and Cordillera el Ronco (Lagunas Khomer Kocha Upper and Lower) allowed for an informed site selection.



**Figure 1.12** The Cochabamba Basin with study locations marked in boxes. Altitudes, historic settlements, strongholds and routes marked. Modified from Sánchez (2008). Inset map locates Cochabamba Basin within Bolivia. Modern Cochabamba city extent not shown.

*Cercado, Cochabamba City - Laguna Alaylay*

The largest lake within Cochabamba city district, Laguna Alaylay, is consistently being impacted by the city's growing population. The lake was deepened and connected to the Rio Rocha in the 1930's, dredged in the early 1990's, and has since suffered from illegal sewage inputs (Ayala et al., 2007 and personal observations). Laguna Alalay, temporarily dried out during the Autumn of 1990 (Ayala et al., 2007). Restoration work that began in June 1997 has begun to act to upon the significant damage caused by sewage input, but clearly the lake's history renders it unsuitable for any palaeo study.

*Chapare, Sacaba - Laguna Larati and Laguna Caluyu*

Situated 1 km apart and only 15 km northwest of Cochabamba city, near the settlement of Larati, both sites presented potential excellent study locations for investigating the impact of ancient human populations. This was reinforced by the subsequently published investigation into the network of Inca trails in the vicinity (Sánchez, 2008) (see Figure 1.12). However, 5 m high dams had been constructed on both sites and, as it was impossible to attain the status of the lakes prior to construction, no further investigation other than surface sediment extraction was conducted.

*Arani, Vacas Lake District – Lakes Parkokocha, Acerokocha, Juntutuyo, Kollpakocha, Challacaba and Yanatama*

The Vacas Lake District is a system of six lakes situated 60 km east of Cochabamba city and 35 km north of the Mizque valley, and is easily accessible by a paved road from Arani (see Section 2.1, Figure 2.1). Ritter (2000), speculated that it is likely that all six lakes within the Vacas municipality would have, at one time, been one large connected system.

Within the Vacas Lake District, Parkokocha is a shallow (1.6–2 m) lake, and the largest by surface area. Initial investigation estimated ~2 m of sediment could be recoverable although sediments were of hard consistency and showed potential signs of periodic desiccation. The second largest lake, Acerokocha, is a deep U-shaped basin probably formed by glacial scouring. The water depth exceeded 12.7 m and therefore proved too deep to core with the equipment available. Lake Juntutuyo and Kollpakocha appear to be hyper-saline lakes today and were therefore rejected. Previous investigation at Juntutuyo suggests it has a maximum depth in excess of 3.5 m (Ritter, 2000), but it was found to

have dried out for a prolonged period prior to 2300 yr BP (Abbott et al., 2003). Lake Challacaba and Yanatama are the smaller lakes in the Vacas system. Lake Challacaba was selected as the most suitable of the Vacas lakes for coring after the preliminary investigations were conducted. A full site description follows in Section 2.1. Yanatama was not investigated due to logistical difficulties and time constraints.

*Chapare, Cordillera el Ronco – Lagunas Khomer Kocha and Khomer Kocha Upper*

This area has vehicle access by an unpaved track leading from the settlement of Aguirre towards Villa Tunari, and is 45 km west of Cochabamba city and 35 km north of the Vacas Lake District (see Chapter 2, Figure 2.5). It is a system of two lakes located on the steep, northeast facing slopes several hours hike from the unpaved track. Laguna Khomer Kocha is the larger of the two water bodies. It is glacially formed. The depth is unknown but suspected to be in excess of 10 m (per. coms. D.Hertel). Laguna Khomer Kocha was not investigated due to the poor accessibility of the site because of the steep, unstable nature of the slopes leading down to the lake shore and the additional time needed to transport the coring equipment. The second lake in the area was previously unnamed, but from here on is referred to as Laguna Khomer Kocha Upper, as it is situated <800 m to the west and approximately 250 m above Laguna Khomer Kocha. Following preliminary investigation, Laguna Khomer Kocha Upper was selected for coring. A full site description follows in Section 2.2.



PROVINCE Municipality Locality	Name	Latitude (S)	Longitude (W)	Altitude (m asl)
CERCADO <i>Cochabamba city</i>	Laguna Alalay	17° 40.027	66° 13.638	~2500
CHAPARE Sacaba	Laguna Larati	17° 20.759	66° 01.121	3576
	Laguna Caluyu	17° 20.889	65° 59.954	3586
ARANI Vacas <i>Vacas Lake Distict</i>	Parkokocha	17° 32.708	65° 38.548	3425
	Acerokocha	17° 35.375	65° 35.745	3423
	Challacaba	17° 33.257	65° 34.024	3419
CHAPARE Villa Tunari - Paracti <i>Cordillera el Ronco</i>	Khomer Kocha Upper	17° 16.514	65° 43.945	4144

**Table 1.2** Location details of the lakes visited in this study during May and June 2007.

#### 1.4.2) Modern ecology

The topographic and climatic variation place the Cochabamba Basin at the confluence of four of the main Tropical Andean ecoregions (Figure 1.4). The ecoregions are the Bolivian Yungas, the Bolivian montane dry forests, the Central Andean Puna and the Central Andean dry Puna. A summary description has already been provided for each (Section 1.1.2). However, the ecological community composition varies with even small lateral and altitude changes. As a result, the vegetation is extremely varied and cannot be easily summarised for the entire Cochabamba Basin and surrounding mountain ranges. Therefore, a more detailed description of vegetation is reserved for later discussion in relation to each specific study site (Chapters 2, 4 and 5).

One of the key features of the vegetation surrounding the Cochabamba Basin is the relative abundance of *Polylepis* woodland. *Polylepis* woodland patches are found at altitudes ranging from 2900–4100 m asl (Hensen, 2002), and so have the ability to survive in many locations throughout the region. Today, many species of *Polylepis* occur in the area, including: *Polylepis neglecta*, *P. sericea*, *P. racemosa lanata*, *P. besseri subtusalbida*, and *P. tormentella incana*, *P.t. incanoides* and *P.t. nana* (Hensen, 2002; Navarro et al.,

2005). Of these, Navarro et al. (2005) also report that the eastern Andes of central Bolivia is the location of endemism for the species of *P. neglecta*, *P. besseri subtusalbida*, *P. racemosa lanata*, *P. tomentella nana* and *P. t. incanoides*. If as previously discussed (Section 1.4.1), a large Pleistocene wetland did exist, the stabilising effect of such a large water body could provide the explanation for the Cochabamba Basin being one of five assumed Andean “refuges” during glacial periods (Fjelds  and Kessler, 1996). If this was the situation, then it may help explain the high levels of endemism seen in the area today.

As well as endemic plant species in the Cochabamba Basin and surrounding mountain ranges, several species of birds, mammals and amphibians also exist solely in this area (Young, 2007). In order to secure the future of this unique flora and fauna, conservation is required. At present, two national parks local to the Cochabamba Basin exists: the Tunari, situated to the north and east (~3300 km<sup>2</sup>, established 1962), and the Carrasco, located to the northwest (~6200 km<sup>2</sup>, established 1991). In addition, the Cochabamba Basin was earmarked by Fjelds  and Kessler (1996) as a first-level conservation priority area. This designation was designed to draw attention to the importance of the *Polylepis* forests and associated habitat, but currently no additional protection of the habitat has been put into place.

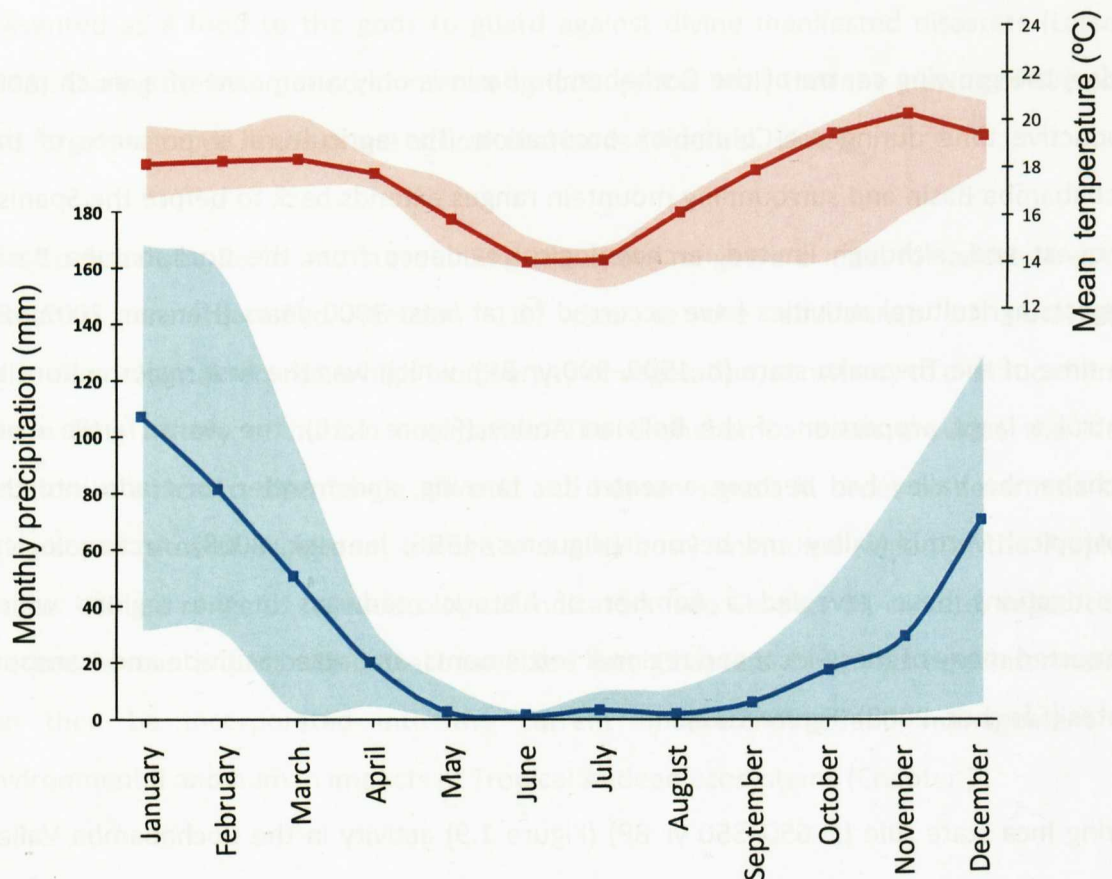
Although *Polylepis* sp. are the dominant constituent of the woodland patches, they exist in a variety of complex communities with other plant species. Hensen (2002), reported that in a survey of 23 different woodland patches, in excess of 250 other species were also recorded either within or in the immediate surroundings. The fauna and flora of the Cochabamba Basin creates a high level of Tropical Andean biodiversity in the locality. As well as the influence of the varied and complex topography, the vegetation of the region is highly sensitivity to any environmental changes.

### 1.4.3) Climate

The climate of the Cochabamba Basin varies considerably due to the pronounced variation in topography. Montes de Oca (2005), reports that Eastern Cordillera regions in general have temperature and precipitation ranges of 16–20°C and 1000–1800 mm/year. In comparison, the Subandean regions at lower elevations experience a more humid climate with temperatures of 20–22°C and precipitation of 1500–2000 mm/year.

However, the climate of the sheltered valleys (e.g. Cochabamba city, ~2500 m asl), is more arid with average annual precipitation of ~480 mm and a temperature range of ~13–19°C (Montes de Oca, 2005). Precipitation shows high seasonal variation, with rainfall greatest during the summer months (December to March) (Figure 1.13).

The Cochabamba Basin and surrounding mountain ranges of the Eastern Cordillera back-arc are highly influenced by changes in inter-annually varying climate systems such as ENSO, and future models predict locally specific adjustments particularly in precipitation amount (Urrutia and Vuille, 2009; Vuille and Werner, 2005).



**Figure 1.13** Monthly average climate data for the Cochabamba Basin, 2000-2009 inclusive. Shaded areas represent minimum and maximum values recorded over the 10-year period. Data provided by Tutiempo Network (2010). Weather station number: 852230 (SLCB), 17° 41.8 S, 65° 10.0 W, 2548 m asl.

#### **1.4.4) Human occupation**

Cochabamba is, today, the principle agricultural region of Bolivia (Larson, 1998). Grains, tubers and coffee are cultivated in the highlands with sugarcane, cocoa beans, tobacco, semi-tropical fruit and coca grown in the more tropical climates of the Bolivian Yungas (Sage, 1984). Compared to other locations in the highlands, crops, primarily the grains wheat, barley and maize, grow well on the fertile soils of the Quaternary deposits, and in the largely temperate seasonal climate of the Cochabamba Basin (Figure 1.13). Geographically, the area lies on an easily accessible trade route between upland and lowland regions, which, in more recent times (since the 1950's), has been exploited by the construction of a number of main arterial roads.

Today, the growing centre of the Cochabamba Basin is only a remnant of a much more productive time during pre-Columbian occupation. The agricultural importance of the Cochabamba Basin and surrounding mountain ranges extends back to before the Spanish conquest and, although limited, archaeological evidence from the Cochabamba Basin suggests agricultural activities have occurred for at least 3000 years (Hensen, 2002). By the time of the Tiwanaku state (c. 1500–900 yr BP), which was the first major culture to control a large proportion of the Bolivian Andes (Figure 1.10), the warm fertile main Cochabamba Valley had become a centre for farming, and frontier for trade into the subtropical Mizque Valley and beyond (Higueras, 1996; Janusek, 2008). Archaeological investigations have revealed a number of historic roadways in the regions which connected many of these local and regional settlements, and acted as trade and transport routes (Sánchez, 2008) (Figure 1.12).

During Inca state rule (c. 650–550 yr BP) (Figure 1.9) activity in the Cochabamba Valley escalated and the area became the largest known Inca production enclave. According to Lone and Lone (1987), the Inca recognised the favourable environmental conditions of the valley and the potential for agricultural opportunities, particularly the cultivation of maize, which exceeded those of all other southern highland locations. Conquering and reorganization occurred, and the replacement/supplement of the local population by 14,000 labourers increased production, particularly in the prime maize valley lands in the western section of the Cochabamba Basin. This restructuring effort saw the Cochabamba valleys become known as the “breadbasket” or “granary” of Bolivia and of the whole

south central Andes, a term that is still used today (Zimmerer, 2000). As well as supplementing the everyday diet of tubers, namely oca (*Oxalis*) and the freeze-dried potato, Chuño (*Solanaceae*), which were grown successfully on the Altitplano, the production of maize (*Poaceae*, *Zea mays*), chilli peppers (*Solanaceae*, *Capsicum*) and squashes (*Cucurbitaceae*; *Cucurbita*) was also successful in the Cochabamba Basin. The presence of storage structures in the archaeological record suggests that growth of these crops was so successful in the Cochabamba valleys that it allowed provisions to be built up for periods of low productivity (Larson, 1998). However, the importance of the Cochabamba Basin and adjoining valleys to the Inca also had symbolic and ceremonial significance. The abundance of maize led to the production of chicha, an alcoholic drink presented as a food to the gods to guard against divine manifested disasters (Larson, 1998). During the Inca period of intense agriculture it is likely that the grazing of livestock was largely reduced in the prime agricultural lands (Wachtel, 1982).

The Cochabamba Basin and surrounding mountain ranges are ideal for addressing the research aims identified (Section 1.3) due to the abundance of obtainable palaeolimnological records, a high biodiversity of vegetation, sensitivity to climatic change and a long history of human occupation. The Cochabamba Basin provides the ideal location in which to disentangle climatic and human signals in order to determine the drivers and rates of ecosystem change in a previously unstudied region of the Tropical Andes. Using a range of palaeoecological indicators (see Chapter 3), climate, vegetation, fire and human impact will be reconstructed (see Chapters 4–6). This new information can then be incorporated into the current understanding and management of environmental and human impacts of Tropical Andean ecosystems (Chapter 7).

### **1.5) Thesis structure and layout**

Following this introductory chapter, this thesis is presented in the form of seven additional chapters that systematically examine the research aims. In Chapter 2 the study sites are described in detail. The geographical setting, modern ecology, climate and human impacts of each location are discussed. Chapter 3 describes the research methods and discusses the rationale and limitations of each technique used in this thesis. This

chapter examines the uses of each analytical technique and provides a summary of the protocols followed.

Chapters 4 and 5 present the main palynological, geochemical and charcoal results and discussion of the two study sites, Lake Challacaba, and Laguna Khomer Kocha Upper. A discussion of chironomid taxonomy notes and taxa discovered is provided in Chapter 6. This section highlights that the published knowledge of Andean chironomid research is in its infancy and shows how this study compliments and builds upon the knowledge gap. Descriptions of the chironomid types discovered are provided and discussed in reference to the data obtained from the sediment cores.

An overall thesis discussion is drawn together in Chapter 7. This chapter, whilst referring to much of the previously presented data from Chapters 4, 5 and 6, places the findings of this thesis into a conservational perspective, focussing on the biogeography of the landscape during the past and likely changes for the future. This chapter applies this new data in by assessing environment sensitivity and vulnerability and how a palaeoecological perspective can inform conservation managers and policy makers. A short summary of conclusions together with recommended future lines of inquiry is presented in Chapter 8.

#### *Year numbering system*

It is commonplace in archaeology to present dates in reference to the start of the Christian era (*i.e.* BC/AD). While this is appropriate for discussions strictly archaeological in nature, when combined with other disciplines time-scales can become confusing. Therefore, throughout this thesis, and following the majority of palaeoecological and palaeoclimatological studies, dates are given as years before present (BP), with AD/BC dates following in brackets where appropriate.



## **Chapter 2) Study sites**

This chapter provides a description of the specific study sites investigated in this thesis. Two locations from the surrounding mountain ranges of the Cochabamba Basin were investigated, Lake Challacaba and Laguna Khomer Kocha Upper. For each site a description of the geographical and geological setting, modern ecology, climatic conditions and human history is provided.

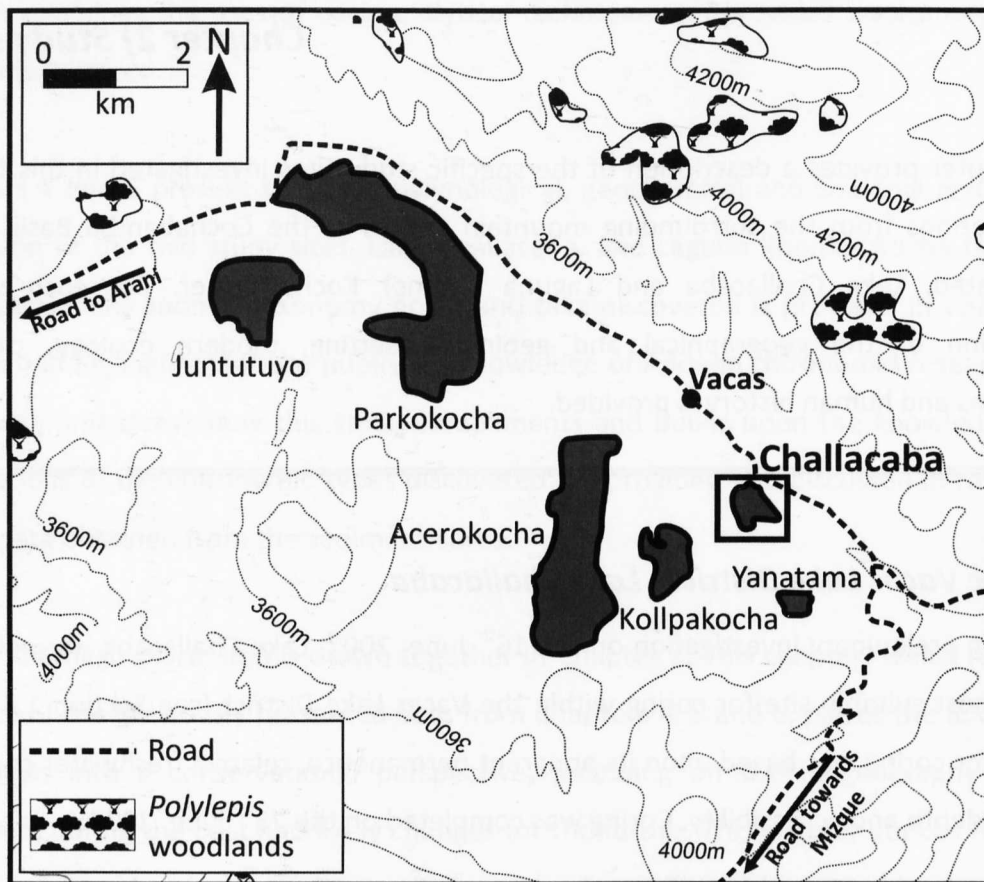
---

### **2.1) The Vacas Lake District - Lake Challacaba**

Following preliminary investigation on the 16<sup>th</sup> June, 2007, Lake Challacaba was selected as the most suitable site for coring within the Vacas Lake District (see Section 1.4). The criteria for coring was based upon its apparent permanence, relative freshwater content, suitable depth and accessibility. Coring was completed on the 23<sup>rd</sup> June, 2007.

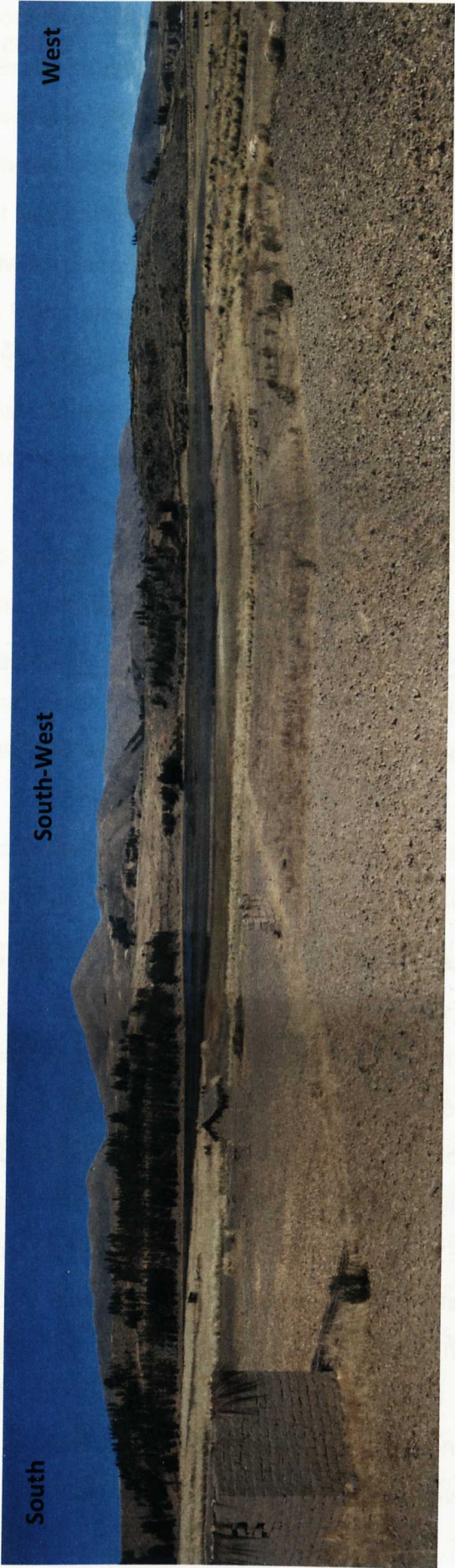
#### **2.1.1) Geographical location and setting**

Lake Challacaba is a small, ~1.5 km<sup>2</sup>, freshwater system, situated at 3419 meters above sea level (m asl) within the cold and dry Vacas valley (17°33.257'S, 65°34.024' W; Figure 2.1). At the time of fieldwork, Challacaba had a maximum water depth of 3 m (Figure 2.2 and Figure 2.3). The lake is approximately 1.2 km in length and 1 km in width, with a total perimeter of ~4 km, and it is aligned northwest to southeast. As previously discussed (Section 1.4.1), it is likely that at several times in the history of the Vacas Lake District, Lake Challacaba was connected to other lakes in the valley, forming one large water body (Figure 2.1). Today however, there is no connection present between the lakes. Instead the lake is fed by an ephemeral stream running off the surrounding mountains to the northeast, and is drained via an outflow at the southeast end. This direct lake input and outflow may explain the freshwater status of the lake in contrast to the increased salinity, due to evaporation, of several of the other Vacas lakes investigated (*i.e.* Acerokocha and Parkokocha). The south and west boundary of the Challacaba lake basin is formed by sparsely vegetated slopes that rise ~70 m and separates Challacaba from Kollpacocha. In contrast the north and east shore is formed by a flatter expanse of land, currently farmed, that would become inundated by water during the wetter months (January–March).

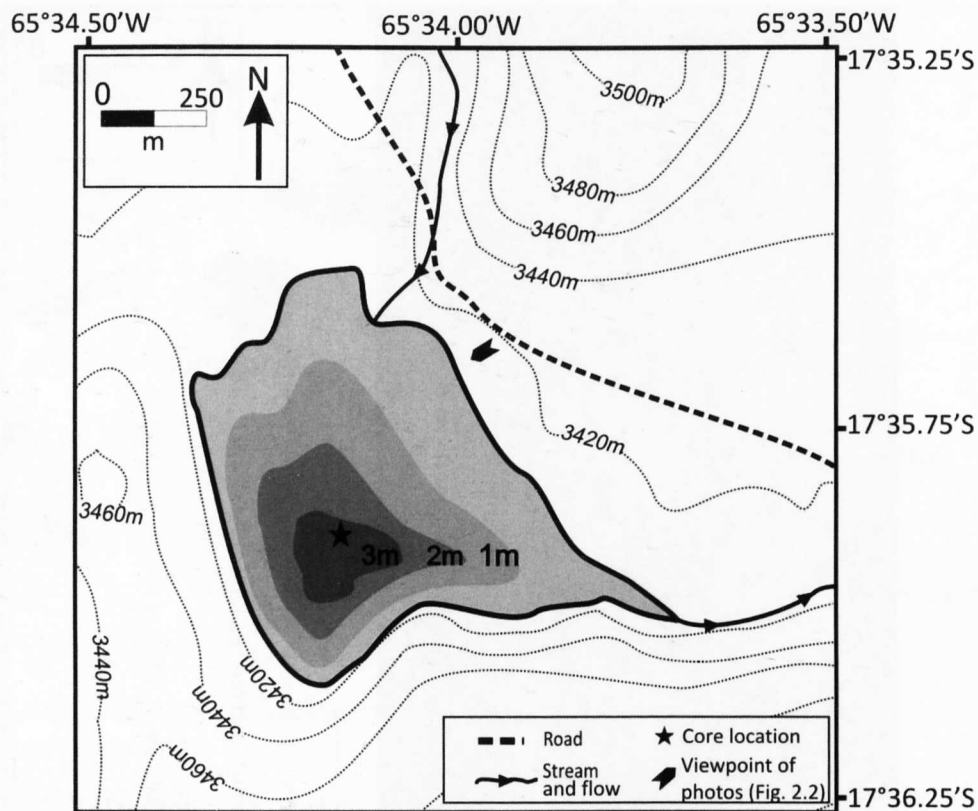


**Figure 2.1** The Vacas Lake District and known *Polylepis* woodlands marked. Black box shows the position of Lake Challacaba (see Figure 2.2 and 2.3). Contour lines represent 200 m.

The local geology is not known in detail but the surrounding high ground consists of Ordovician (488.3–443.7 Ma) quartzite and sandstone that is a common feature along the length of the Eastern Cordillera (see Section 1.1.1 and 1.4.1). The Vacas valley is most likely to have been formed within Quaternary sedimentary deposits, similar to the main Cochabamba Basin, but no detailed study is available and the causes of lake formation for Challacaba and all in the Vacas lakes remains unknown. It is likely however, that several lakes, most obviously Acerokocha, were created during previous glacial events, as attested to by the deep glacial scour nature of the lake basins. If the lakes were once connected, the separation, due to reduced water levels, may have been because of a decrease in hydrological input or the opening up of an outflow channel. However, with erosion a major feature of Andean landscapes, we suggest that deposition of material originating from the surrounding hillsides might also have played a significant role in separating the lakes.



**Figure 2.2** Composite photograph of Lake Challacabá, Vacas Lake District. Photograph taken from northeastern shore looking south (far left of image) to west (far right of image). Recently planted fast growing trees (*Eucalyptus*) on far southern shore. Mudbrick (adobe) huts and farmed land at forefront (northwest shore). Location from which the photograph was taken is shown in Figure 2.3.



**Figure 2.3** Map of Lake Challacaba and local topographic features. Contour lines at 20 m intervals. Lake depths determined by bathymetric survey (see Section 3.1).

### 2.1.2) Modern ecology

Lake Challacaba and the other lakes within the Vacas District are positioned within the Central Andean Puna ecoregion (see Chapter 1). Further vegetation classification has been achieved on a regional scale for Bolivia. The Vacas Lake District has been regionally classified as being within the “northern Puna–semi-humid” (Ibisch et al., 2003) and “sub–humid Puna and Punean woodlands of the Tunari” (Navarro and Maldonado, 2002) biogeographic regions. Additionally, Navarro and Ferreira (2007) produced a digitised vegetation map of Bolivia (scale 1:250000), with field verification, that currently offers the most detailed description of vegetation. This database is importable into applications such as ArcGIS and GoogleEarth and so exact locations can be pinpointed. This classification identifies the lake vegetation of great importance for livestock. The vegetation of the surrounding lands can be summarised as sub–humid ranging from grassland, shrubland, saxicolous vegetation to *Polylepis* forest (Navarro and Ferreira, 2007).

Important botanical families of the Vacas Lake District and surroundings include Asteraceae, Brassicaceae, Bromeliaceae, Caryophyllaceae, Gentianaceae, Poaceae and Rosaceae (Montes de Oca, 2005; Navarro and Ferreira, 2007). While these classifications are a broad-brush approach, they can offer insight into the dominant vegetation types and potential vegetation communities. Although not conducted in the Vacas vicinity, Navarro and Maldonado (2002; pg 248-251) offer a more detailed description of the flora typical of the Vacas biogeographic zone, suggesting the importance of genera including: *Poa*, *Festuca*, *Deyeuxia*, *Muhlenbergia*, *Stipa* (all Poaceae), *Gomphrena* (Amaranthaceae), *Baccharis* (Asteraceae), *Polylepis* (Rosaceae), *Peperomia* (Piperaceae), *Astragalus* (Fabaceae) and *Puya* (Bromeliaceae).

There are no terrestrial vegetation surveys available for the Vacas area. However, previous studies on the aquatic vegetation of Acerokocha, Juntutuyo, Kollpakocha and Parkokocha are available (see De la Barra, 2003; Molina et al., 2007). Of note from these studies is the finding that *Zannichellia andina* and *Potamogeton striatus* (both Potamogetonaceae) are indicators of saline or hypersaline conditions, and so their relevance to the freshwater system of Challacaba may be limited. From our own observations of aquatic vegetation at Challacaba, it was clear that *Myriophyllum* spp. was one of the dominant components. Therefore, the lakes organic input is likely to come from the abundance of aquatic plants, together with other terrestrial sources.

As with the main Cochabamba Valley (see Section 1.4.2), the relatively flat lands surrounding the Vacas lakes appeal to human occupation, and today the area is heavily impacted by humans (Navarro and Ferreira, 2007). In 2001, the settlement of Vacas had a population of 650 (Instituto Nacional de Estadística, 2002). The flat Vacas valley floor is dominated by the cultivation of potatoes and other tubers, barley, beans and oats (Gotkowitz, 2007; Montes de Oca, 2005). The remaining land is Andean grassland that has been heavily damaged by grazing of cattle and goats. Some planted *Eucalyptus* trees are present on the steeper slopes (Figure 2.2), most likely in an attempt to stabilize the soil and provided a source of building material, but the timing of planting is unknown. Planting of this exotic tree is a common practice across Bolivia and Peru (Fjeldså and Kessler, 1996).



Further away from most directly human impacted lands, and more typical of the vegetation of the surrounding mountains ranges of Vacas, the landscape consists of *Polylepis* woodland patches within Andean grassland. Remnants of *Puya raimondii* exist within the *Polylepis* woodlands and grassland matrix (Navarro and Maldonado, 2002). Studies of the *Polylepis besseri* woodlands at Sacha Loma (17°44' S, 65°34' W; ~3800 m asl, 16 km south of Challacaba) have provided a detailed inventory of species found within them (Fernández, 1997; Fernández et al., 2001). The most local *Polylepis* woodland patches are located ~5 km away in the mountains to the northeast, and ~10 km to the southwest (Figure 2.1). Our own observations of a small *Polylepis nana* stand by the side of the Arani to Vacas road (17°33.540' S, 65°42.329' W; 3379 m asl), revealed tree heights of 1–1.5 m growing in patches along the edge of a rocky field boundary.

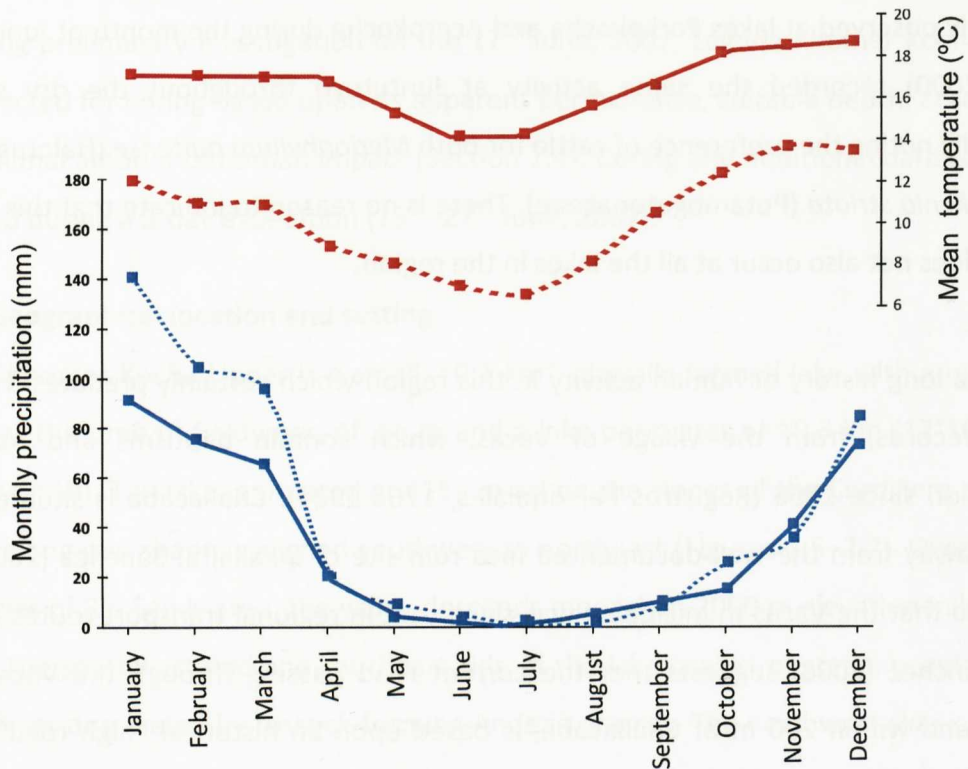
### 2.1.3) Climate

The nearest meteorological station to the Vacas Lake District is located at Arani (17°34' S, 65°46' W; 2865 m asl) (see Figure 1.12). This station is situated 22 km west of the study site and at 314 m lower elevation in the Cochabamba Basin proper. Mean temperature and monthly precipitation data for the Arani meteorological station is provided (Figure 2.4).

As no local instrumental metrological data are available for Challacaba, interpolations of observed data (1950-2000) from closest weather stations provides an estimate of the values for sub 1 km grid squares (Hijmans et al., 2005). Analysis of this data set within the GIS package DIVA shows that at Lake Challacaba during the dry season (June–August) precipitation averages 2.6 mm/month and increases to 114 mm/month for the wettest three months (January–March). Annual temperature varies from 7.2°C to 11.3°C for the wet and dry season respectively. Total annual precipitation is estimated from the interpolated data at 537 mm (Figure 2.4).

Comparison between the interpolated data for Challacaba and the metrological data for Arani shows relative agreement in precipitation. Similar trends are also observed in the mean temperatures although the Arani metrological data is offset by an increase of ~5°C. This difference is in part representative of the variation in altitude (314 m).





**Figure 2.4** Monthly average climate data for the Vacas Lake District and surrounding area. Interpolated data for Challacaba (dashed lines) from Hijmans et al. (2005). Meteorological data for Arani (17°34' S, 65°46' W, 2865 m asl) (solid lines), from Gareca et al. (2010).

#### 2.1.4) Human occupation

Lake Challacaba is situated 2.5 km south of the settlement of Vacas (Figure 2.1). Like the rest of the Vacas Lake District, flatter workable lands (*i.e.* for Challacaba those on the northern shore), are worked up to the water's edge (Figure 2.2). The inundation of this land during the wetter months may help to replenish some of the soil nutrients lost through farming processes. The vegetation of the Vacas valley is noted as being dominated by crops in the national vegetation classification (Navarro and Ferreira, 2007). Set back from the road by a distance as little as a 200 m, the lake is easily accessible today and several small farm buildings are positioned between the lake and the road (Figure 2.2).

In addition to the farmed land, the lakes are also used as a source of water and feed for livestock. The importance of the Vacas lakes for the herding of goats and cows was noted

in the national vegetation classification (Navarro and Ferreira, 2007), and this activity was personally observed at lakes Parkokocha and Acerokocha during the month of June 2007. Ritter (2000) recorded the same activity at Juntutuyo throughout the dry season, specifically noting the preference of cattle for both *Myriophyllum quitense* (Haloragaceae) and *Stuckenia striata* (Potamogetonaceae). There is no reason to indicate that this animal grazing does not also occur at all the lakes in the region.

There is a long history of human activity in this region which certainly predates the local church records, from the village of Vacas, which contain baptisms and marriage information since 1766 (Registros Parroquiales, 1766-1924). Challacaba is situated only ~15 km away from the well-documented Inca ruin site of Inkallajta. Sánchez (2008) has suggested that the Vacas municipality was significant in regional transport routes (Figure 1.12). Sánchez (2008) suggests that the current road passing through the Vacas Lake District, and within 200 m of Challacaba, is based upon an historical “high road”. This road was one of the principle routes that connected the main Cochabamba Valley to the smaller peripheral settlements.

Routes were established between the fuertes (strongholds) of Inca Rakay in the west, to those in the east and southeast such as Inkallajta, Comarapa, Pulquina and Samaipata. The important Tiwanaku archaeological site of Mizque (Figure 1.12; Higuera, 1996) was also connected to the main Cochabamba valley by the establishment of well used routes. Given the importance of camelid pastoralism and caravans for pre-Columbian peoples (Lynch, 1983), and the movement of Tiwanaku traders between the main Cochabamba valley and the Mizque enclave (Janusek, 2008), it seems likely that many pre-Incan groups would also have done so, using the same routes the Inca’s claimed at a later period. As a result many pre-Columbian cultural groups moving or trading between the Cochabamba valley and Mizque or Inkallajta would have been in direct contact with Challacaba and the Vacas lakes. Therefore Challacaba has likely experienced a long history of human impact on varying scales.

## **2.2) Laguna Khomer Kocha Upper**

Following preliminary investigation on the 17<sup>th</sup> June, 2007, Laguna Khomer Kocha Upper was selected for coring based upon its apparent permanence, suitable depth, accessibility and minimal amount of human impact (Section 1.4). Coring and additional data collection occurred during a 3-day expedition (25<sup>th</sup>–27<sup>th</sup> June, 2007).

### **2.2.1) Geographical location and setting**

Laguna Khomer Kocha Upper is a small,  $\sim 0.1 \text{ km}^2$ , glacially formed lake with a maximum depth, at the time of fieldwork, of 3.6 m and a lake perimeter of  $\sim 0.3 \text{ km}$  ( $17^\circ 16.514' \text{ S}$ ,  $65^\circ 43.945' \text{ W}$ ). The lake is situated at 4153 m asl on the slopes of the Cordillera el Ronco and its elongated shape is aligned southwest to northeast (Figures 2.5–2.7). Over looking tributaries of Rio San Mateo, the valley descends more than 2000 m elevation in less than 10 km. The southwest end and southeast side of the lake consist of steep, vegetated but stable faces dominated by tussock-forming Andean grasses. The northwest side is created by an apparent glacial deposit (lateral or median moraine) of around 2 m in height running the length of the lake ( $\sim 120 \text{ m}$ ). This moraine separates the lake from an area of flat, waterlogged, ground which is likely to represent an infilled lake of similar size to Laguna Khomer Kocha Upper (see Figure 2.6 and 2.7B).

While there are no obvious fluvial inputs, Laguna Khomer Kocha Upper is likely to be fed by runoff from the step situated above the back wall and subterranean seepage from the small catchment area. At the time of coring the lake was a closed basin, however, an outflow channel at the north eastern end (Figure 2.7A),  $\sim 0.25 \text{ m}$  above the current water level, provides a partial breach of the moraine. Once past this point, water would descend down the steep forested gully towards larger lake of Laguna Khomer Kocha ( $\sim 3900 \text{ m asl}$ ; Figure 2.6).

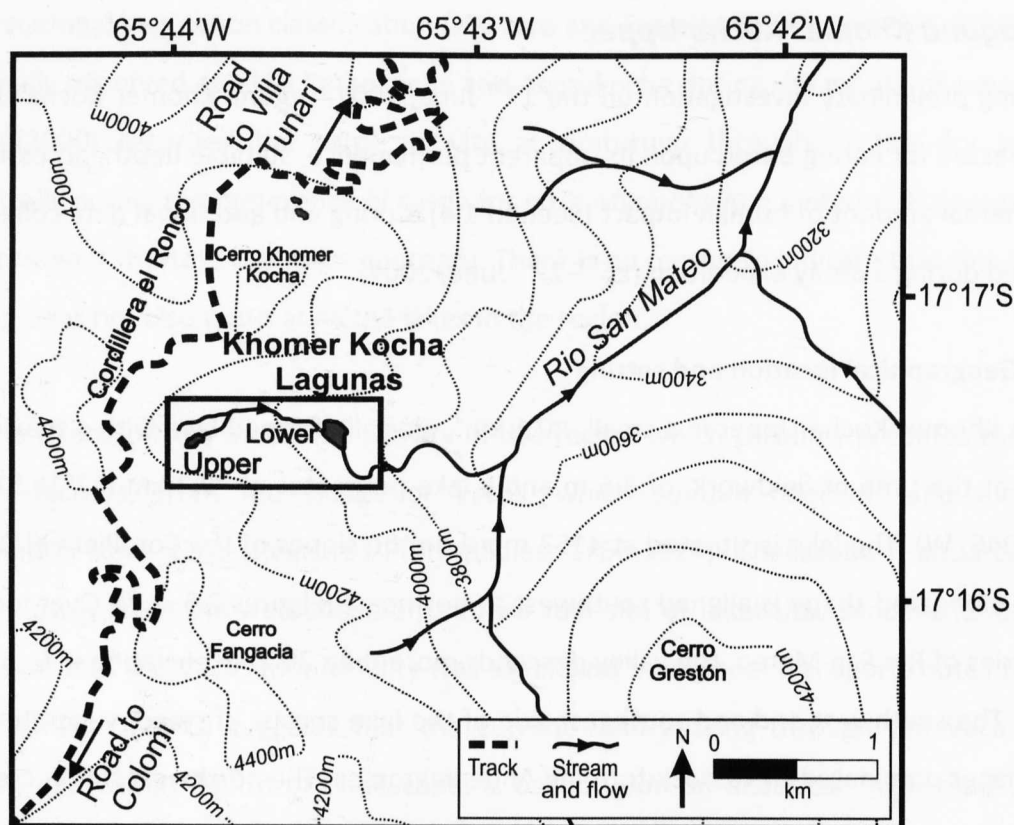


Figure 2.5 Map of the Khomer Kocha area and local features. Road, watercourses and mountain ranges shown. Contour lines are at 200 m intervals.

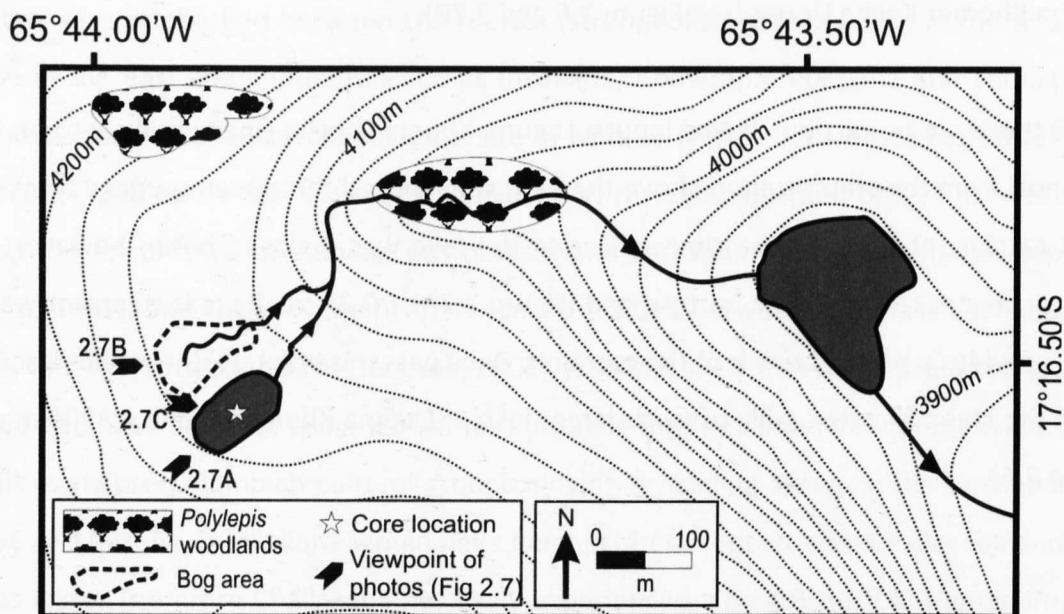
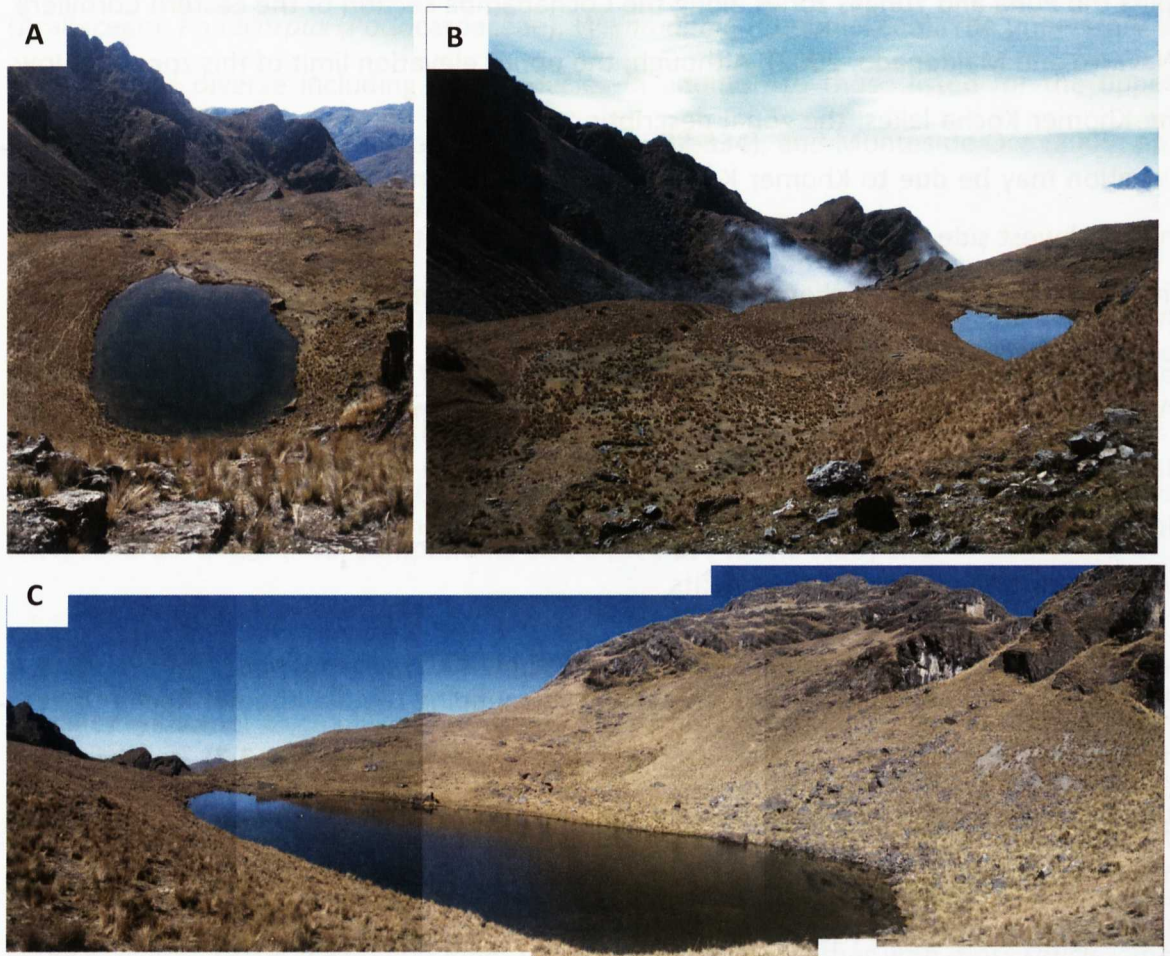


Figure 2.6 Map of the Khomer Kocha Lagunas (upper and lower). Local terrain, investigated *Polylepis* woodlands and lake inputs/outflows shown. Waterlogged ground shown as dashed line area. Contour lines at 20 m intervals. Photograph locations correspond to Figure 2.7.



The site specific geology is not known in detail, but a study conducted at a lower elevations on the same range, found the bedrock material to consists mainly of sandstones, lutites and quarzitic rocks of Ordovician (488.3–443.7 Ma) and Devonian (416.0–359.2 Ma) age with areas of granite intrusions. Calcareous rocks were found between 2000–2200 m elevation (Kessler, 2002b). There are mountain peaks in the local area that reach heights in excess of 4500 m elevation but no permanent snow patches were evident. Above ~4300 m elevation, large proportions of the landscape were dominated by rock exposures together with large stone blocks scattered throughout the vicinity.



**Figure 2.7** Laguna Khomer Kocha Upper. **A)** The lake looking from above toward the northeast. **B)** The lake looking from above towards the east. The area of waterlogged ground is clearly evident. Cloud formation in the valley moving moisture upwards. **C)** Composite photograph of the lake looking southeast and clearly showing the steep back walls. The locations from which the photographs were taken is shown in Figure 2.6. Photographs A and C provided by William Gosling.

### 2.2.2) Modern ecology

Positioned within the Bolivia Yungas ecoregion (see Chapter 1), the lagunas of Khomer Kocha lie in a region of rapid changes in ecology in association with elevation. The Bolivian specific classifications of Ibisch et al.'s (2003) and Navarro and Ferreira (2007) position the lakes between the biogeographic regions of the Bolivian Yungas, and the Northern semi-humid Puna. Navarro and Maldonado (2002) offer a more detailed description of the biogeography, and suggest that the site lies in the "transitional humid to sub-humid Punean woodlands".

The transitional humid to sub-humid Punean woodlands, is a biogeographic zone that splits the Puna and Yungas zones along the Cochabamba section of the Eastern Cordillera (Navarro and Maldonado, 2002). Although, the upper elevation limit of this zone is below the Khomer Kocha lakes, the zonal description otherwise fits well, and the offset in the elevation may be due to Khomer Kocha receiving sufficiently more rainfall than sites on the southwest side of mountain ranges where the description is primarily acquired from. This biogeographic zone is characterised by genera including: *Polylepis* and *Hesperomeles* (both Rosaceae), *Berberis* (Berberidaceae), *Ribes* (Grossulariaceae), *Schinus* (Anacardiaceae), *Baccharis* and *Mutisia* (Asteraceae) and *Escallonia* (Escalloniaceae). Navarro and Maldonado (2002), note that this assemblage of vegetation can connect to a riparian meso-tropical forest habitat, where *Vallea* (Verbenaceae) and *Alnus* (Betulaceae) become important floristic components.

On a local scale, the flatter lands immediately surrounding Laguna Khomer Kocha Upper, in particular the adjacent area of water logging (see Figure 2.6 and 2.7), can be most suitably characterised as a hygrophilous Puna meadow. Genera common of these areas include: *Festuca*, *Deyeuxia* and *Poa* (Poaceae), *Eleocharis* (Cyperaceae) *Juncus* (Juncaceae), *Ranunculus* (Ranunculaceae) *Hypocoeris*, *Werneria* and *Perezia* (Asteraceae), and *Trifolium* (Fabaceae) (Navarro and Maldonado, 2002).

Below the lagunas of Khomer Kocha the upper limits of the Yungas montane forest extend up the valley of Rio San Mateo. The upper Yungas vegetation has an elevational limit of 3700–4200 m asl, dependant on local microclimatic conditions. The local vegetation classification is "upper Yungas of the Chapare" which is characterised by the



genera: *Polylepis pepeii* (Rosaceae), *Gynoxis* (Asteraceae), *Pentacalia* (Asteraceae), *Ribes* (Grossulariaceae), *Berberis* (Berberidaceae), *Bomarea* (Alstroemeriaceae), *Salpichroa* (Solanaceae) and *Fuchsia* (Onagraceae). Companion genera include: *Oxalis* (Oxalidaceae), *Luzula* (Juncaceae), *Cajophora* (Loasaceae), *Solanum* (Solanaceae), *Perizia* (Asteraceae) and *Festuca* (Poaceae), together with species of bryophytes and ferns (Navarro and Maldonado, 2002).

At lower elevations (3100–3700 m), the lower Yungas of the Chapare, is characterized by the tree genera of including: *Polylepis racemosa lanata* (Rosaceae), *Clethra* (Clethraceae), *Escallonia* (Escalloniaceae), *Ilex* (Aquifoliaceae), *Myrsine* (Myrsinaceae), *Oreopanax* (Araliaceae), *Podocarpus* (Podocarpaceae), *Weinmannia* (Cunoniaceae). The understory is complex and diverse including many species in addition to those listed for the upper Yungas. See Navarro and Maldonado (2002; pp. 332-334), and Montes de Oca (2005; pp. 209-210) for a species inventory.

A feature that can be quickly determined from the above biogeography and vegetation discussion is the complexity of the Khomer Kocha ecology. The correct definition for the study location probably lies within a combination of the Puna and transition woodlands. However, with such a steep elevation gradient present in the valley of San Mateo, it is likely several Yungas floral components also exist close to the study site.

A study by Hertel and Wesche (2008) in September 2003 represents the only known study specific to Khomer Kocha lake area. Here, the authors reported a *Polylepis lanata* stand (3650 m asl) with a secondary tree layer dominated by *Oreopanax macrocephalus* (Araliaceae) and *Baccharis pentlandii* (Asteraceae), together with *Fuchsia* and ferns. At higher elevations (3800 and 4050 m asl), *Polylepis pepeii* stands were identified with the genera *Gynoxis* (Asteraceae) and *Ribes* (Grossulariaceae), together with moss species and the herbaceous genera *Luzula* (Juncaceae) and *Bomarea* (Alstroemeriaceae).

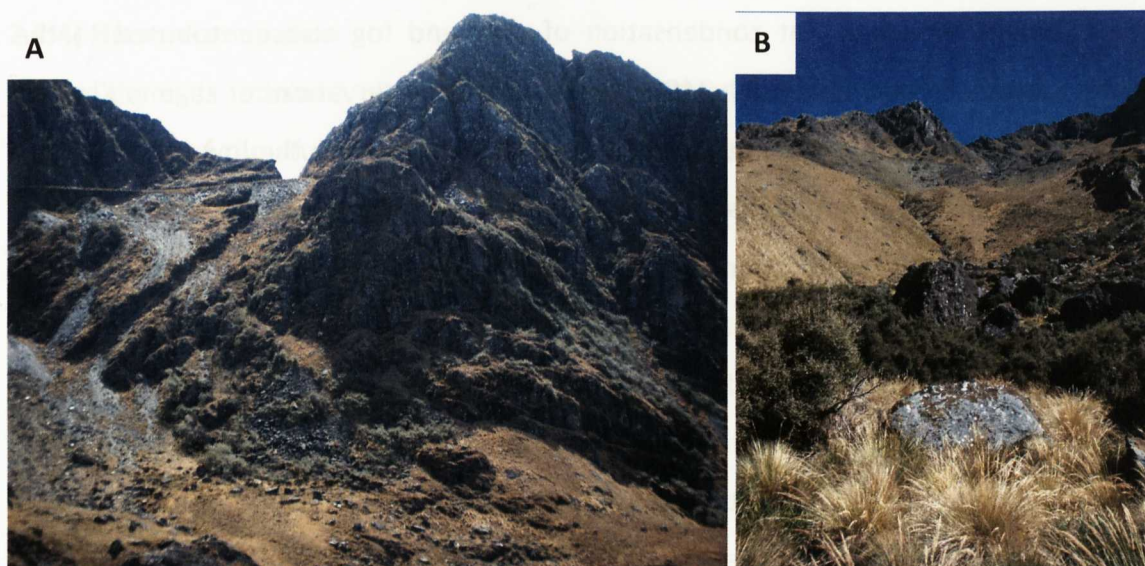
The only other information from the vicinity is reported by Navarro and Maldonado (2002; p. 333), from observations during field study that:

“...on the laguna of Khomer Kocha; dense forest, little intervention (human impact), with 6–8 m canopy, covered with epiphytic bryophytes on trunks and branches” (Translation from Spanish).

Navarro and Maldonado (2002), also note large extensive mats of *Isoëtes lechleri* (Isoetaceae) that form in shallow, cold waters of Laguna Khomer Kocha. In addition, the authors record the presence of the peaty grassland genera of *Deyeuxia* (Poaceae) and *Senecio* (Asteraceae), and the wetland species of *Plantago tubulosa* (Plantaginaceae).

Our observations of the study location found two *Polylepis* woodland patches in close proximity to Laguna Khomer Kocha Upper (Figure 2.6). One patch, 300 m to the north, was located at the base of an exposed rock face within a screefield with large stone blocks present (Figure 2.8A). The ground is steeply sloped and unstable which made access difficult. The ground appeared well drained and the vegetation, where not *Polylepis*, was limited to tussock forming grasses.

The second woodland patch was found in the gully below Laguna Khomer Kocha Upper and ~400 m northwest (Figure 2.8B). Although the gully was positioned at the base of a screeslope, the woodland here was located on flatter ground that had a small stream flowing through. Large blocks of stone were also scattered amongst the trees and high growing varieties of grasses and rushes were abundant in areas of waterlogged ground near to the stream (Figure 2.8B). The *Polylepis* woodland was dense and tangled which made access difficult (see Figure 1.6B). Individual trees were covered in mosses, a phenomenon not observed at the first site, indicating increased moisture. As reported by Hertel and Wesche (2008), several tree and scrub species were also present, although in sporadic and lower abundances.



**Figure 2.8** The *Polylepis* woodlands around Laguna Khomer Kocha Upper. **A)** Above the lake looking north. Screeslopes are clearly evident. **B)** Below the lake looking west, amongst large boulders and high growing grasses in the waterlogged ground.

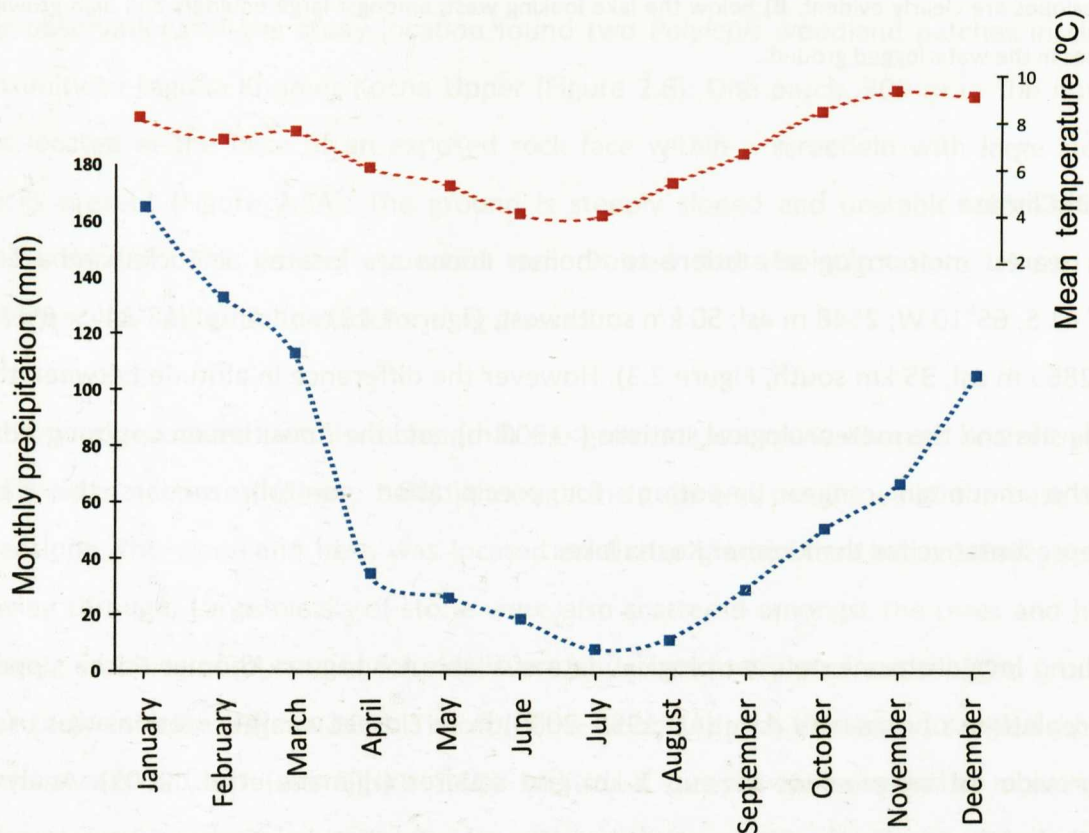
### 2.2.3) Climate

The nearest meteorological stations to Khomer Kocha are located at Cochabamba City ( $17^{\circ} 41' S$ ,  $65^{\circ} 10' W$ ; 2548 m asl, 50 km southwest, Figure 1.13) and Arani ( $17^{\circ} 34' S$ ,  $65^{\circ} 46' W$ ; 2865 m asl, 35 km south, Figure 2.3). However the difference in altitude between the study site and the meteorological stations ( $>1300$  m), and their position on opposing sides of the mountain ranges (important for precipitation control), renders the data unrepresentative for the Khomer Kocha lakes.

With no local instrumental metrological data available for Laguna Khomer Kocha Upper, interpolations of observed data (AD 1950–2000) from closest weather stations was used to provide estimate values for sub 1 km grid squares (Hijmans et al., 2005). Analysis concluded that during the dry season (June–August) precipitation averages 13 mm/month and increases to 138 mm/month for the wettest three months (January–March). Mean temperature varies from  $4.5^{\circ}C$  to  $7.6^{\circ}C$  for the wet and dry season respectively. Total annual precipitation is estimated at 772 mm (Figure 2.9).

Kessler (2002b) reported that condensation of dew and fog also contributed to the humidity, especially between 1600–3400 m asl. Our own observations at Laguna Khomer Kocha Upper (June 2007) show that cloud gradually ascends from the low valleys to the northwest. As a result, large quantities of moisture are deposited on the vegetated slopes, as high as ~4100 m asl, even during the dry season.

Short-term climatic conditions at Khomer Kocha were investigated during the month of September 2003. Daily temperature ranges were recorded at altitudes of 3850 and 4050 m asl and yielded values of  $-0.6^{\circ}\text{C}$  to  $11.5^{\circ}\text{C}$  (mean of  $3.4^{\circ}\text{C}$ ), and  $-2.3^{\circ}\text{C}$  to  $9.5^{\circ}\text{C}$  (mean of  $1.7^{\circ}\text{C}$ ) respectively (Hertel and Wesche, 2008). These results indicate a lapse rate of  $\sim 0.5^{\circ}\text{C}$  per 100 m elevation gain.



**Figure 2.9** Monthly average climate data for the Laguna Khomer Kocha. Interpolated data from Hijmans et al. (2005).



#### 2.2.4) Human occupation

Today there is minimal sign of human impact at Laguna Khomer Kocha Upper. Investigation of the study site surroundings revealed one small rock shelter near to the track that would be sufficient for 1–2 people, and a small herd of 7 semi-wild horses. Examination of the *Polylepis* woodland patches surrounding the lake revealed no indications of exploitation (*i.e.* cutting for fuelwood, burning or excessive browsing). At lower elevations (<4000 m asl) minimal human impact was also observed, although the grassland around the lower lake showed evidence of recent burning in August 2003 (Hertel et al., 2008; D. Hertel, 2010 pers.coms).

The lagunas of Khomer Kocha are situated on the boundary of Carrasco National Park and although not included within the parks management, information regarding modern human practices are likely to relate. Today the current population for the whole ~6200 km<sup>2</sup> of Carrasco National Park is estimated to be around 100 families who reside in the low elevation Yungas environments and use the land for farming, cattle herding and agroforestry. Potential crops in the Puna environment include tubers, oats, wheat, barley and quinoa, with coca, corn, maize and yucca among those produced in the lowlands of the Yungas (ParksWatch, 1996). The nearest agricultural fields were ~15 km away by road.

Although there are the remains of a small Inca sites (Inkachaca; 15 km west; >2000 m lower elevation; Figure 1.12), there is no direct route available from the lake site due to the steep topography. The ancient road network (Sánchez, 2008; Figure 1.12) that passed through the Vacas Lake District and connected much of the Cochabamba Basin area (see Section 2.1.4), also connected to Inkachaca. However, there is no indication of an ancient roadway near Khomer Kocha and the lake is difficult to access due to site remoteness, altitude and unstable terrain. The track used to access the study area today passes within 1 km of Laguna Khomer Kocha Upper, but is 200 m above the site (see Figure 2.5). It is the old, now unused track that leads from Cochabamba city to Villa Tunari, via ‘Cuevas del Repección’ and passing along the western limits of Carrasco National Park (Kessler, 2002b). Often described by the name “camino a las nubes” (“road to the clouds”), it is today impassable and closed in the lower elevations of the Yungas due to vegetation regrowth since the opening of a new road that runs farther to the west. While we cannot

rule out previous higher levels of human impact from just visual examination of the lakes and surrounding, there is no evidence to suggest a greater extent occurred in the past.

### **2.3) Conclusions**

The two study locations provide an ideal situation in which to address the aims set out in Section 1.3. Lake Challacaba's location upon an ancient road network provides the long-term historical information of human occupation of the region. This information is needed to be able to disentangle natural environmental changes from those initiated by human activity. In contrast, the relative natural state of the landscape surrounding Laguna Khomer Kocha Upper allows the assessment of the vegetation dynamics, including the *Polylepis* woodlands, without the impacts of extensive human occupation. The different climatic conditions and biogeographies at Lake Challacaba and Laguna Khomer Kocha Upper will allow an examination of relative sensitivities and vulnerabilities of the local environment at each location to changes in the climate system. As both lakes are similar sizes, the accumulation of ecological deposits into the sediments should be from comparable spatial scales.



**Chapter 3)****Field and laboratory methods and analytical techniques**

This chapter presents the research methodologies and discusses limitations of the laboratory and statistical techniques employed during this doctoral research. All fieldwork was completed during the months of May and June 2007 in Bolivia. Laboratory preparation and analysis was conducted from 2007–2010 at The Open University. In addition to the methodologies discussed here, detailed analytical protocols and examples of preparation and recording sheets are provided in Appendix A2.

**3.1) Lake observations and data recording**

Conductivity, pH, depth and turbidity were recorded for each study site to provide a direct indication of conditions represented in the most recently deposited sediments (*i.e.* top 0–1 cm) (Table 3.1). A basic bathymetric survey of each lake site was completed using a handheld sonar to establish maximum lake depth. Depths were recorded along a transect line passing from the shore to the centre of the lake until the deepest section was located. The position of each depth measurement was marked via the use of a handheld GPS. Next a 2.5 cm diameter core of the top 0.5–1 m of sediment was extracted and examined. This test core provided an indication of the substrate type and allowed an initial assessment of the suitability of the site before the full coring rig was deployed. Measurements of conductivity, pH and turbidity were recorded using handheld devices, as described in Table 3.1.

Variable	Method	Instrumentation used
Water conductivity	$\mu\text{S}/\text{cm}$ (microSiemens per cm)	Hanna 991300 handheld probe
Water acidity	pH	Hanna 991300 handheld probe
Water depth	Bathymetric survey	HawkEye Digital Sonar DF2200PX
Water turbidity	Secchi depth	White anchor bag

**Table 3.1** Methods and instrumentation used to measure Bolivian lake variables during the 2007 field season. A detailed protocol for use of the Hanna probe and for water sampling is provided in Appendix A2.

## **3.2) Lake sediment coring procedures**

### **3.2.1 Long core**

All long sediment cores were extracted using a cam-modified Livingstone piston corer (Livingstone, 1955; Wright et al., 1984), belonging to the Open University's Palaeoenvironmental Change Research Group (OU-PCRG). The coring platform consisted of two Avon inflatable tender boats with a lightweight wooden platform secured across them (Figure 3.1). The platform was secured in position at three points to anchor bags. An extra inflatable was used where possible for storage of additional casings, rods and tools. The coring procedure, together with example designs for platform construction is fully described by Colinvaux et al. (1999).

The deepest part within each lake was located by initial bathymetric survey as previously described in Section 3.1. Coring at the deepest part increased the chances of obtaining the longest available sediment core, and reduces the probability of encountering a phase in the sediments when the lake dried out. Following deployment of the full coring rig, two overlapping sediment cores, positioned 1–2 m apart, were obtained. The overlap was used to ensure that any material that may have been lost from the bottom of one core is safely encased in the middle part of the overlap core. It also allows subsampling of core ends, where contamination may be higher, to be avoided. During the fieldwork for this project the team of three was able to raise two (~5 m) cores from 3 m of water in one full day. Sediments are encased within aluminium core tubes of either 50 or 38 mm diameter, and raised in 1 m long sections (drives) where they are then sealed using caps and tape, and carefully labelled. They were then kept horizontal and flown back to The Open University's cold storage facility (4°C).

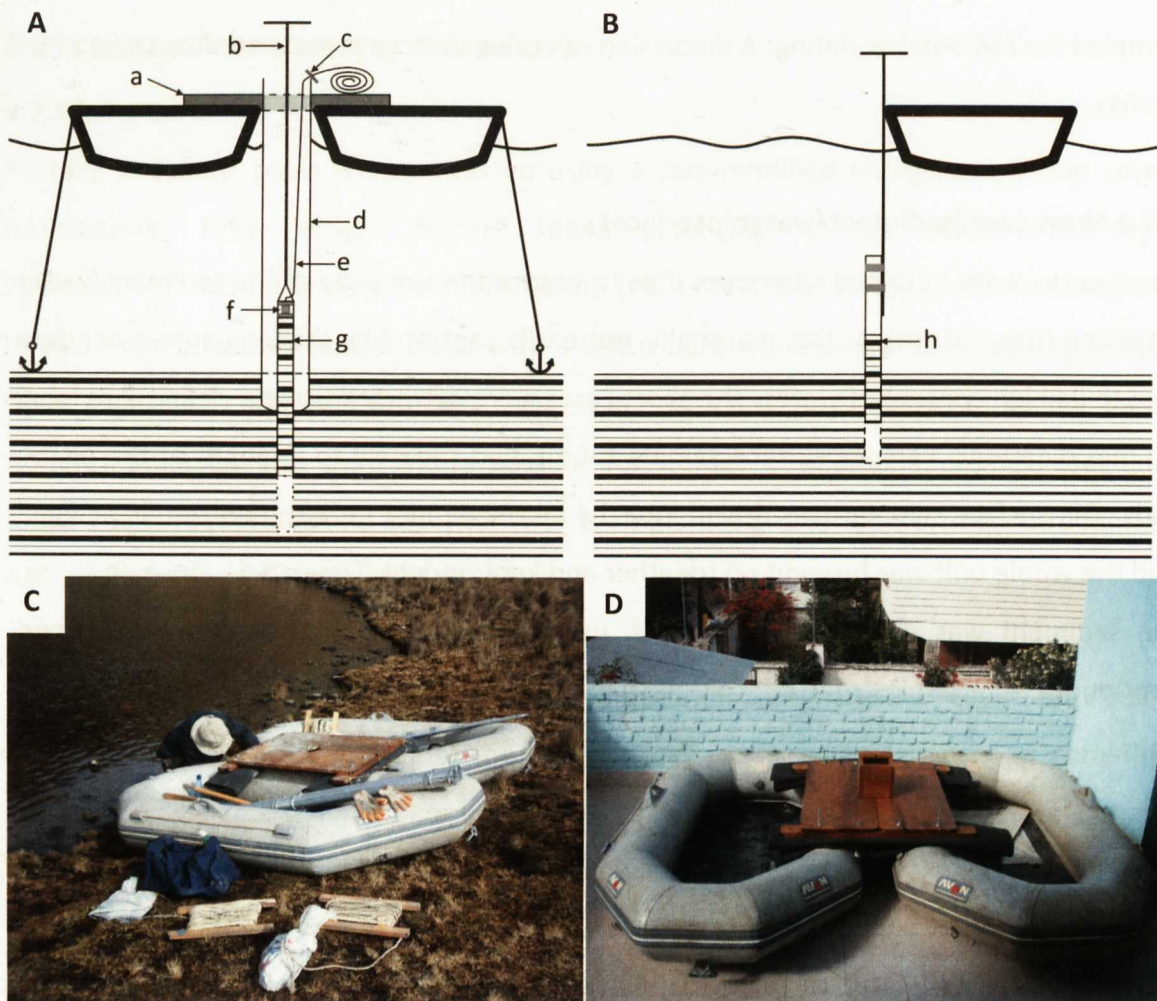
The Livingstone coring procedure chosen prevents a preliminary examination of the sediment in the field. This can be considered a disadvantage when the nature of the sediment, or success of the coring drive is unsure. However, coring systems that keep samples encased until such time when contamination risk is reduced (*i.e.* in the laboratory), is a significant advantage. This not only reduces potential errors in the ecological proxies to be examined, but also limits the exposure of material that is later

sampled for radiometric dating. A discussion of coring devices is presented by Glew et al. (2001).

### **3.2.2 Short core (sediment/water interface)**

Short cores were obtained where possible to ensure the sampling of the sediment/water interface (top ~50 cm), as this material is not easily captured by the long core procedure due to its high content of water. The short cores were extracted using a clear 1.2 m long, 50 mm diameter, Perspex surface sample tube taped securely to a length of the piston rods. The surface sampler was driven into the lake sediment until the bottom is plugged and the whole unit was brought up together and kept upright (Figure 3.1). Once on shore, the sediment was extruded in the field, using a bung (piston) and pusher rod, and continuous subsamples of 1 cm thickness were transferred into labelled plastic sample bags.





**Figure 3.1** Diagrams and photographs of coring setup. **A)** long core. **B)** short core. **C)** and **D)** platform for long core. Labelled parts in A and B are:

- a) Wooden platform bridging the boats – circular hole in platform allows for the casing to pass through and be clamped in place.
- b) Coring rods and T-bar – used for pushing the core tube into sediment and to extract the unit.
- c) Cable clamp – allows the exact depth when sediment capture begins to be determined by the operator.
- d) Casing – remains clamped to coring platform throughout and penetrates into the sediment thus allowing coring tubes to relocate the initial core hole created during the previous drives.
- e) Cable – to determine the drive depths. Remains attached to piston mechanism for emergency retrieval.
- f) Piston mechanism – this is positioned at the bottom of core tube until the desired depth for sediment to be contained, thus preventing erroneous material from entering the tube.
- g) Aluminium core tube barrel – are exchanged after each 1 m drive. Diagram A shows the full core tube during extraction, leaving empty the core hole for subsequent drives to pass freely down.
- h) Perspex surface core tube barrel secured with the use of tape to the coring rods – only driven part way into sediment thus preserving the sediment/water interface within the core tube. The unit is then transported vertically back to the shore for sampling.

### **3.3) Sample logging, documentation and subsample extraction**

#### **3.3.1 Core splitting**

The sediment cores were split using a router with a titanium drill bit, on a specifically designed bench mounted tube holder. Using interchangeable parts, the holder is capable of clamping both the 38 and 50 mm diameter, 120 mm long aluminium core tubes. Cutting of both sides was completed in several sweeps by gradual lowering of the drill bit until a thin layer, a little thicker than 0.1 mm, remains. Once grooves on both sides of the tubing had been reduced to this thickness the final cut through the tubing was made using the clean blade of a retractable knife. The sediments encased within the cut tubing were then split using clean wire held at tension and, where necessary, parted using a clean pallet knife. When not being examined, the cores were wrapped in two layers of plastic wrap and kept horizontal in cold storage at 4°C. See Appendix A2.2 for the full protocol.

#### **3.3.2 Description and cataloguing**

Once split, all the cores were immediately photographed and described. This took place before processes which may affect the appearance of the core surface can occur; e.g. iron oxidation, cracking due to drying, mould growth. The sediments were described using the Troels-Smith system (Birks and Birks, 1980). Colour was recorded using the Munsell Soil Colour Chart (2000). Any macrofossils suitable for radiometric dating were noted and extracted (see Section 3.5 for details).

In the absence of a core scanner facility, overlapping photographs of each core section were taken and processed to provide one image per core drive. To ensure maximum clarity and detail of the core photographs, several methodologies of photography were tested (see Appendix A2.3). Two methods, numbers 5 and 6, were subsequently utilised and the method for composite photographs is described below. Details of the other methodologies tested are given in Appendix A2. The system developed aimed to maximise colour details recorded, improve consistency between photographs and minimise any limitations of the camera.

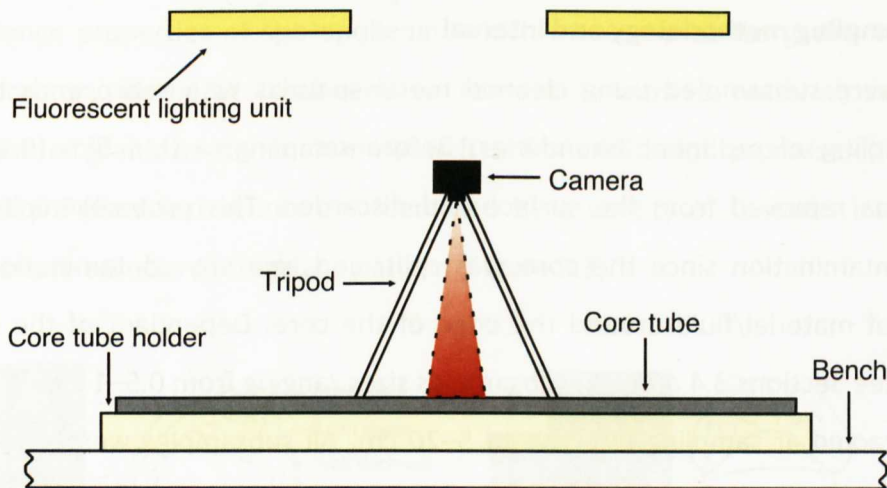
### *Photographic set up and capture*

A Kodax V610 Dual Lens digital camera was held 90 cm above the core surface on a tripod that allowed for downward facing photography (Figure 3.2). The camera was set to 6.1 megapixel resolution, a lens zoom of  $\times 3$  and the exposure adjusted to 3 seconds. Black sheet paper was positioned underneath the length of the core to provide a uniform background colour and an example card of the Munsell Soil Color Chart (2000) positioned in shot to allow for later calibration if required. Photographs of  $\sim 10$ – $20$  cm overlapping sections were taken using a 3 second timer to minimise movement of the camera.

Lighting settings created the greatest challenge in the procedure. To produce a homogenous illumination as possible, room lighting (two sets of fluorescent strip lights) was used with the core positioned between the two light sources. It was found that these produced a more uniform illumination than spotlights, which had a tendency to increase shadowing where the core surface was uneven, and rapidly begin to dry out the core. However, fluorescent rooms lights are not suitable for all situations, especially when precise image analysis is to take place, as they rapidly cycle through a range of colour temperatures (Nederbragt et al., 2006). While they therefore do not provide a perfect solution, for this study it was found that once the lighting increased in stability, after  $\sim 20$ – $30$  minutes, it provided the most suitable and uniform option available.

The photography of a wet core also created additional problems. Dependant on sediment type, several cores allowed water to collect on the surface more readily. While McMillian (2008) reports that wet cores often produces the clearest images of sedimentary structure, the non-uniform reflection created, particularly towards the image edges, often rendered the photographs unusable. To mitigate this problem, the number of photographs taken was increased, thus only making the most central portions of each photograph used in the composite. Another option to alleviate this problem is the use of a polarising filter (Lamoureux and Bollmann, 2005; Nederbragt et al., 2006), but one was not available for use with this camera.





**Figure 3.2** Schematic diagram of the photographic set up used in this study. Red triangular area shows limits of each photograph.

#### *Creating a composite image*

Photographs were stitched together using Corel Photo-Paint 13 with 'Blend Value' set to 'O'. Blending cannot be used as it alters the individual pixels thus preventing any future image analysis. The software utilised allows an image to be made temporarily transparent so that it can be superimposed onto the existing image and aligned correctly. Once in place both images are combined and the next image in the sequence superimposed as before. While the process is time consuming and requires a high level of user interface, the result allows for easier future presentation and analysis. The writing of algorithms that recognise and position overlapping images would be beneficial in increasing time effectiveness, although thorough checks would still need to be made.

Since the cores used in this study were documented, McMillian (2008) published a guide to producing a simple, low cost core-imaging system, utilising a regularly available handheld digital camera. Another process discussed by McMillian (2008) worth implementation, is the automated batch cropping of photographs to specified dimensions. This process is performed by several image programs which automatically remove any unwanted backgrounds in the photographs and reduces the image file sizes considerably. Additional information on image analysis is provided by Saarinen and Petterson (2001), and Francus (2005).

### **3.3.3 Sub-sampling methodology and interval**

The cores were subsampled using cleaned metal spatulas with sharp ends to enable precise sampling of sediment boundaries. Before sampling, a thin film (0.1 mm) of sediment was removed from the surface and discarded. This protocol minimises any airborne contamination since the core was split, and also any contamination due to movement of material/fluid around the edge of the core. Dependant of the analytical procedure, see Sections 3.4 and 3.6, subsamples sizes ranging from 0.5–1 cm<sup>3</sup> and 0.5–1.5 g, were extracted at sampling intervals of 5–20 cm. All subsamples were sealed within labelled 15 or 50 ml disposable centrifuge tubes that would be used in the chemical preparation. Where subsamples were taken in advance of chemical preparation, centrifuge tubes were kept sealed in the cold storage facility (4°C) until required. The sampling procedure for chronological determination differs to that described above (see Section 3.5).

## **3.4) Analysis of ecological proxies**

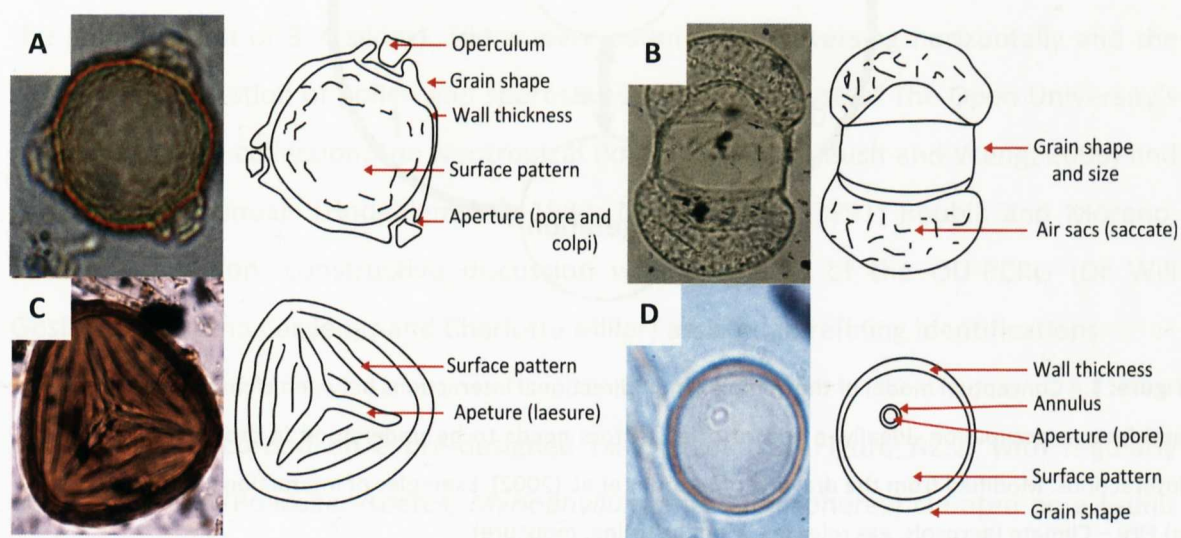
### **3.4.1 Fossil pollen and spores**

#### *Rationale for use*

Fossil pollen and spore (Figure 3.3.) analysis has provided a principle method for understanding the Earth's ecological and climatic history since its initiation by von Post (1929; 1946). The importance of palynology, the study of fossil pollen and spores, lies in the reconstruction of vegetation in response to natural and anthropogenic forced environmental changes (Figure 3.4). Palynology can provide valuable insight into these vegetation responses by analysis of the microscopic fossil specimens contained within of range of deposits of varying duration and resolution. Examples include, but are not limited to; annual lake varve records of the Holocene (e.g. Wick et al., 2003), silica sinter deposits from geothermal field fluctuations (Martin et al., 2000) and time snapshots within carbonaceous shales of the Early Cretaceous (e.g. Brenner, 1996).

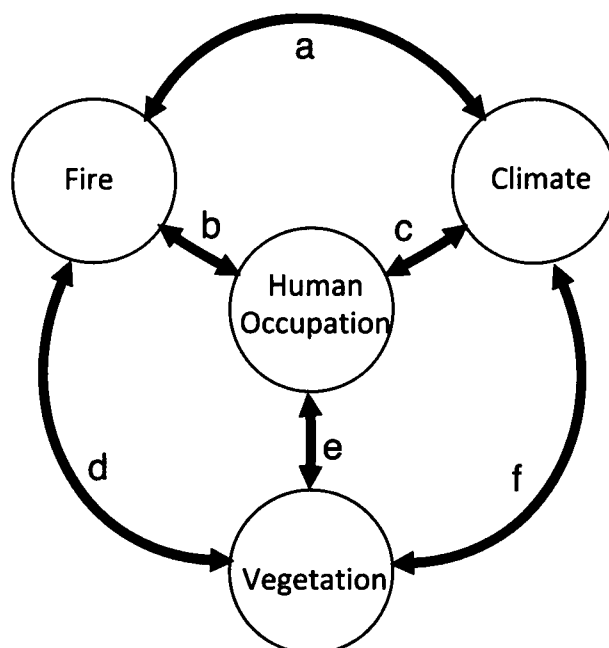
Palynological studies provide the majority of our past knowledge about the central Andes. This is primarily due to the abundance and well preserved nature of pollen and spores, found in lake, marine sediments, ice cores, cave deposits and exposed sections.

The resistance properties of sporopollenin, which makes up pollen grains walls, allows harsh laboratory chemical treatment to remove unwanted material, and enables preservation of grains in any environments free from oxidation processes (Bennett and Willis, 2001). Pollen and spores are identified by a variety of features including size, shape, aperture number and surface pattern (Figure 3.3).



**Figure 3.3** Morphology of pollen grains and spores. Key structures and sculpture that are commonly used to identify types. Images are of specimens identified in this study. **A)** *Polylepis/Acaena* type. **B)** *Podocarpus*. **C)** Trilete spore. **D)** Poaceae.

Simple reconstruction of environmental conditions dominated early palynological investigation. However, in more recent years, and in response to questions focussing around mans' influence on the global and local environment, and the potential global changes we have to adjust to, the focus of research has shifted. As a result, detailed, high resolution research into environmental thresholds (Willis et al., 2010), invasive species management (MacDonald, 1993), abrupt climate changes (e.g. 8200 yr BP event; Alley and Ágústsdóttir, 2005), and the protection of threatened ecosystems (Burney and Burney, 2007) are just a few examples of the type of research questions being addressed.



**Figure: 3.4** Conceptual model of the complex multidirectional interactions between climate, vegetation, fire and human occupation. Ideally, a record of all factors needs to be understood in order to interpret the interactions. Modified from the drawing of Brenner et al. (2002). Examples of interactions include:

- a) Fire – Climate (aerosols, gas release - wind, lightning, moisture)
- b) Fire – Human (hazards – clearance, regime control, ignition)
- c) Human – Climate (emissions – lifestyle, resource availability, location choice)
- d) Vegetation – Fire (fuel – growth patterns)
- e) Human – Vegetation (clearance, selectivity, growth patterns – location choice, resource supply)
- f) Climate – Vegetation (temperature, moisture – gas exchange, albedo)

### Methodology

From both the Challacaba and Khomer Kocha Upper cores, a subsample of 0.5–1 cm<sup>3</sup> was extracted from the core on average every 10 cm for pollen and fungal spore analysis. Pollen concentration was determined by the use of a spike prior to chemical preparation. Due to the natural occurrence of many of the typically used exotic pollen/spore spikes (*Lycopodium*, *Eucalyptus* and *Alnus*), synthetic 16 µm diameter microspheres were added at a 1:2 ratio of the subsample (*i.e.* 0.25–0.5 cm<sup>3</sup>). Microspheres were provided by the LacCore facility (Batch 2, lot number 150907). Subsequent chemical preparation followed standard palynological protocol (Faegri and Iversen, 1989). A full detailed protocol and example tick sheet is provided (Appendix A2.4; Figure A2.1).

Samples were mounted on microscope slides in glycerol which allows easy rotation of grains. Pollen and spores were identified using a Nikon Eclipse 50i microscope at  $\times 400$  and  $\times 1000$  magnification. For a discussion on identification techniques see Bennett and Willis (2001). In all cases a minimum of 300 fossil terrestrial pollen grains were analyzed in each sample or, where pollen concentrations were exceptionally low, counting was continued until 3000 microspheres of the added spike were counted (regularly requiring the identification of 3–4 slides). Slides were counted by traversing horizontally and the singular identification of pollen and spores was achieved by use of The Open University's pollen reference collection, the Neotropical Pollen Database (Bush and Weng, 2006) and other pollen manuals (Hooghiemstra, 1984; Moore et al., 1991; Roubik and Moreno, 1991). In addition, constructive discussion with members of the OU-PCRG (Dr Will Gosling, Macarena Cardenas and Charlotte Miller) assisted in refining identifications.

Counts were recorded on a pre-designed tally sheet (see Figure A2.2) with regularly occurring types (*Poaceae*, *Isoëtes*, *Myriophyllum* and microspheres) counted on a 5-unit manual cell counter. All unique types were digitally photographed for reference purposes using a Lumenera Infinity 1 digital camera and the image capture software ImageJ (Rasband, 1997-2009). A digital copy all photographs is provided in Enclosure CD1 and full taxa list is given in Appendix A4.1 (Tables A4.1 and A4.2).

### *Limitations*

Like the majority of lake-based palaeoecological studies, palynology began as fundamentally a qualitative discipline. However, its application remains highly appropriate in answering many modern ecological questions from a range of temporal and spatial scales (Willis and Birks, 2006). In addition, the rapidly expanding range of numerical modelling that can now be utilised with palaeoecological data is improving the application of results, and ensures the perception of the discipline now centres as a quantitative analytical science (Birks, 1985; Birks, 1998; Birks and Gordon, 1985). At the heart of this development is growing computing literacy and available software, some of which is open source and/or specific to palaeoecological data (e.g. PaleoMAS). See Bennett and Willis (2001) for a general overview and Correa-Metrio et al. (2010) for a recent Andean application.



Nonetheless, as detailed by Lowe and Walker (1997), several important assumptions about palynology remain. These must be understood and, where possible, accounted for during data interpretation. These can be summarized into two main themes. First, that present-day environmental factors governing species' distribution have not changed and that these present/past distributions represent populations that are/were in equilibrium with the present/past governing environmental factors. In addition, there is a requirement that former plant and animal distributions have modern analogues today that represent their ecological traits. And second, that there is no bias from the processes of preservation and analysis. Therefore, the fossil assemblage extracted is an accurate representation of the assemblage originally deposited and that no differential destruction or contamination occurs, including during laboratory preparation. Also, the identity of remains must be established to a sufficient taxonomic precision and consistency.

Light microscopy allows the identification of pollen types frequently only to family level, using variations observed in structure and sculpture (*i.e.* size, shape and pattern) (see Figure 3.3). Increased taxonomic precision to genus or species is highly dependant on regional diversity and the availability of a reference collection and/or specific keys. Although, as with fossil chironomid analysis (Section 3.4.3), there may also be offset between the apparent and actual information gained with increasing taxonomic resolution (Figure 3.8). As a result analysts must be cautious when assigning identification to pollen types and in response a range of conventions are now used to indicate certainty in identifications. For example, the suffix "type" is used to acknowledge there is at least one other alternative (Bennett and Willis, 2001).

Of specific relevance to this study, the identification of *Polylepis* pollen from the genus *Acaena* (both Rosaceae) poses a difficulty due to morphological similarities. However, previous studies argue that a confident separation of two genera is achievable due to geographical and habitat restrictions (Chepstow-Lusty et al., 2005; Gosling et al., 2009; Weng et al., 2006). Another example of complication in Andean taxa identification is the split of Chenopodioideae (previously Chenopodiaceae) from Amaranthaceae. In the literature, many studies group the types as Chenopodiaceae/Amaranthaceae



(Cheno/Ams) due to similarities in the periporate morphology. However, the discussion receives continued attention due to importance of crop pollen (quinoa) from the genus *Chenopodium*, which is considered an indicator of pre-Columbian human occupation (Bush et al., 2005; Chepstow-Lusty et al., 2003; Valencia et al., 2010). Throughout this study the nomenclatures “*Polylepis/Acaena* Type” and “Cheno/Ams” are used, as ultimately identification can only be certain with scanning electron microscopy (see Smit, 1978). These and other taxonomic precision complications are discussed (Chapters 4 and 5). Additional discussion on the principles, techniques, advancements, applications and limitations of palynology are readily available (Bennett and Willis, 2001; Faegri and Iversen, 1989; Moore et al., 1991; Traverse, 1988).

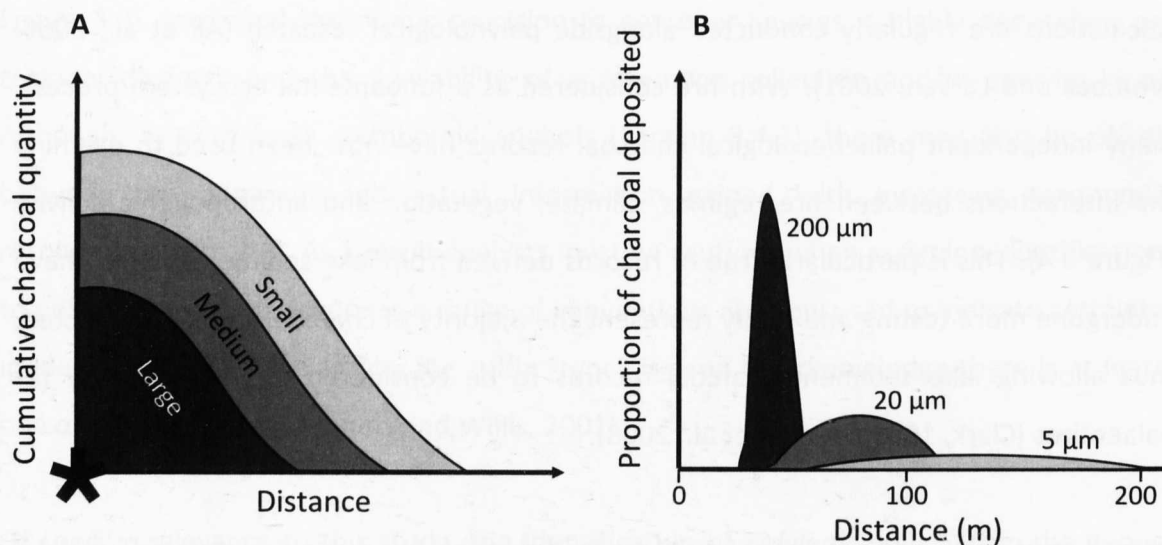
### 3.4.2 Charcoal

#### *Rationale for use*

Since the development of charcoal abundance studies, predominantly but not exclusively by Clark and colleagues (Burney, 1987; Clark, 1988a; Clark, 1988b; Clark, 1988c; Clark et al., 1998; Clark and Patterson, 1997; Clark and Royall, 1995; Cwynar, 1978), fire regime calculations are regularly conducted alongside palynological research (Ali et al., 2009; Whitlock and Larsen, 2001). With fire considered as a fundamental ecosystem process, many independent palaeoecological charcoal records have now been used to examine the interactions between fire regimes, climate, vegetation and anthropogenic activity (Figure 3.4). This is particularly true of records derived from lake sediments, which have undergone more testing and today represent the majority of charcoal studies conducted, thus allowing lake sediment charcoal records to be considered as a good proxy for palaeofires (Clark, 1988a; Power et al., 2008).

As well as understanding the processes by which charcoal becomes incorporated into lake basins, research has been conducted into the relationship between particle size and atmospheric residence time (Clark and Royall, 1995). Particles of different size classes will travel different distances in the air column (Figure 3.5), with larger particles travelling much less distances before they are deposited (Whitlock and Larsen, 2001 and references within). With this in mind, and with the scope of this study to examine the local ecosystem changes, with particular focus on the impacts to high Andean woodland,

charcoal analysis was only conducted on macroscopic particles  $>100\ \mu\text{m}$ . Particles of this size are not deposited far from the fire source by aeolian transportation;  $<7\ \text{km}$  (Whitlock and Millspaugh, 1996),  $<50\ \text{m}$  in alpine environments (Tinner et al., 2006). However, distances are dependant on a variety of factors including fire intensity, size and severity (Whitlock and Larsen, 2001), and debate remains regarding the actual distances over which fall-out occurs (Higuera et al., 2007). Care must also be taken when interpreting fluvial deposits, especially of large river systems as transportation distance can be much greater. Larger macroscopic particles have been shown to detect changes in fire regimes that are often unnoticed in microscopic (pollen slide count) analysis (Clark, 1988c). It is understood that pollen processing methods (e.g. acetolysis), can darken non-charcoal plant remains, increasing uncertainty of counts (Blackford, 2000). While microscopic particles can be a useful record of regional burning signals (up to hundreds of km's from source) (Ali et al., 2009), they were not analysed in this research due to the scope of the study focussing on impacts on the local spatial scale.



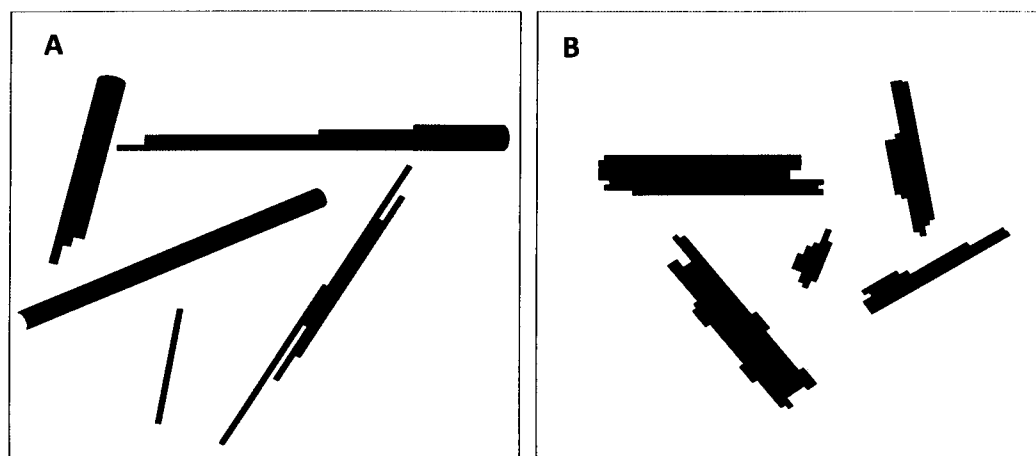
**Figure: 3.5** Models displaying the relationship between charcoal particle size and distance before deposition. **A)** Purely conceptual graph modified from Patterson et al. (1987). Fire source at marked by an asterisk. **B)** Percent of charcoal deposited at distance from fire source. Based upon a wind speed of  $3\ \text{m}\cdot\text{s}^{-1}$  and a convection column height of 10 m. Modified from Clark (1988b).

Several different methods now exist for the enumeration of macroscopic charcoal within a sample; number (number of particles/cm<sup>3</sup>), area (mm<sup>2</sup>/cm<sup>3</sup>) and volume (mm<sup>3</sup>/cm<sup>3</sup>), which can be achieved through a variety of procedures including counting, weighing or digital image analysis. Whitlock and Larsen (2001) suggested that despite the differences in the methodologies, they tend to produce similar results, a conclusion further supported by a recent comparative study of lake sediment records (Ali et al., 2009). These findings add confidence to our interpretations when comparing charcoal abundance records calculated via different methods, and for this study all charcoal analysis was accomplished via the manual counting of individual charcoal particles.

### *Methodology*

Where possible (but dependant on sediment availability), charcoal analysis was conducted at the same sampling resolution as pollen and spores. Subsamples of 1 cm<sup>3</sup> (0.5 cm<sup>3</sup> in one sample) were deflocculated with 10% potassium hydroxide (KOH) for 24 hours before being sieved and separated into two size fractions (>180 µm and 100–179 µm). Samples were then suspended in water on a gridded Petri dish and counted using a binocular dissecting microscope (Olympus SZX12) at typically ×12.5 up to ×25 magnifications. Abundances were recorded onto a pre-designed tally sheet prior to digital data entry (Appendix A2.5).

Charcoal particles are readily identified by the angular structure, opacity, the reflective black surfaces (Clark and Royall, 1995) and by obvious fragmentation when pressed. In this study, a distinction was also made between two particle morphotypes. Elongate particles, often flatter or maintaining a semi-circle shape (which can be seen easiest at ends), with smoother edges were classified here as type 1 (herbaceous/grass type). Type 2 (wood) is characterised by particles with angular and irregular shape, that are often denser in appearance and display cell structure especially after breakage (see Figure 3.6).



**Figure: 3.6** Sketch drawings of the two charcoal particle morphotype groups defined in this study. **A)** Type 1: Elongate particles, often flatter or maintaining a semi-circle shape with smoother edges were (herbaceous/grass type). **B)** Type 2: Angular and irregular shaped particles, often denser in appearance and may display cell structure especially after breakage (wood type).

### *Limitations*

Although non-charred material resembling charcoal particles is often encountered during macroscopic analysis, the combination of defining factors, as listed previously, enables particles to be readily identified with time and practice. Identification is also aided by the manual counting method as each particle can be individually checked by the analyst if unsure (*i.e.* breaking, light adjusting, etc...). With identification and analytical methodological problems aside, the major limitations of charcoal analysis focus on sampling resolution, the separation of fire events from a background noise signal, and the defining the locality of events. Each of these is discussed in reference to the study presented here (Chapters 4 and 5).

The separation of charcoal particle morphotypes executed during this study does have additional limitations. An insufficient number of publications exist that display images of spilt charcoal types (Enache and Cumming, 2006; Jensen et al., 2007; Walsh et al., 2008) and those that do, demonstrate a need for a reference collection of site specific, experimentally charred specimens before material type can be defined. Therefore, while in this research charcoal particles are separated into types, the source material of each type, whilst insightful, remains unconfirmed.

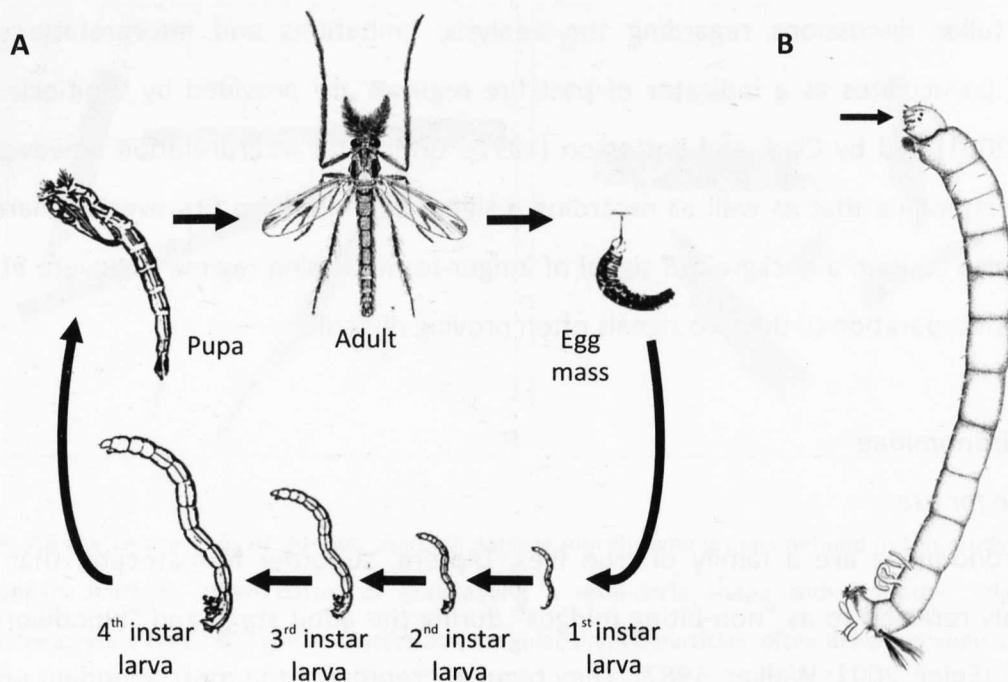
Several fuller discussions regarding the analysis, limitations and interpretations of charcoal particulates as a indicator of past fire regimes are provided by Whitlock and Larsen (2001) and by Clark and Patterson (1997). Critical for interpretation however, is the understanding that as well as recording a signal of short term fire events, charcoal records also contain a background signal of longer-term burning regimes (Higuera et al., 2007) with separation of the two signals often proving difficult.

### 3.4.3 Chironomidae

#### *Rationale for use*

The Chironomidae are a family of true flies, Diptera, suborder Nematocera, that are commonly referred to as “non-biting midges” during the adult stage and “bloodworms” as larvae (Epler, 2001; Walker, 1987). They regularly represent the most abundant group of macroinvertebrates found in fresh and saltwater habitats and have a worldwide distribution, exploiting vast elevation and temperature ranges (Armitage et al., 1995; Ashe et al., 1987; Ferrington, 2008; Pinder, 1986). The life cycle of chironomids (Figure 3.7A) involves four stages (instars) as larvae with each stage culminating in moulting and the shedding of an exoskeletal cuticle (Walker, 1987). Of the integuments shed, the heavily sclerotised chitinous head capsule (Figure 3.7B and 3.8) becomes well persevered within lake sediments, particularly those of the 3rd and 4th instars (Velle et al., 2010; Walker, 2001).

The suitability of chironomids for palaeoecological studies is due to several characteristics in addition to their good preservation and abundance in lake sediments as previously discussed. With the majority of species stenotopic, chironomids are highly sensitivity to changes in environmental conditions. Together with many genera exhibiting short life cycles (quick generation time) and being mobile as adults (carried on winds), chironomids are able to rapidly track environmental changes (Brooks, 2005; Walker, 2001).



**Figure 3.7 A)** Chironomid life cycle (not to scale). Composed and modified from the drawings of Borror et al. (1976), Walker (1987) and Epler (2001). Adult species shown is *Dicortendipes thanatogratus* (Epler, 2001). **B)** A Chironominae larva. Head capsule position shown. Modified from Epler (2001).

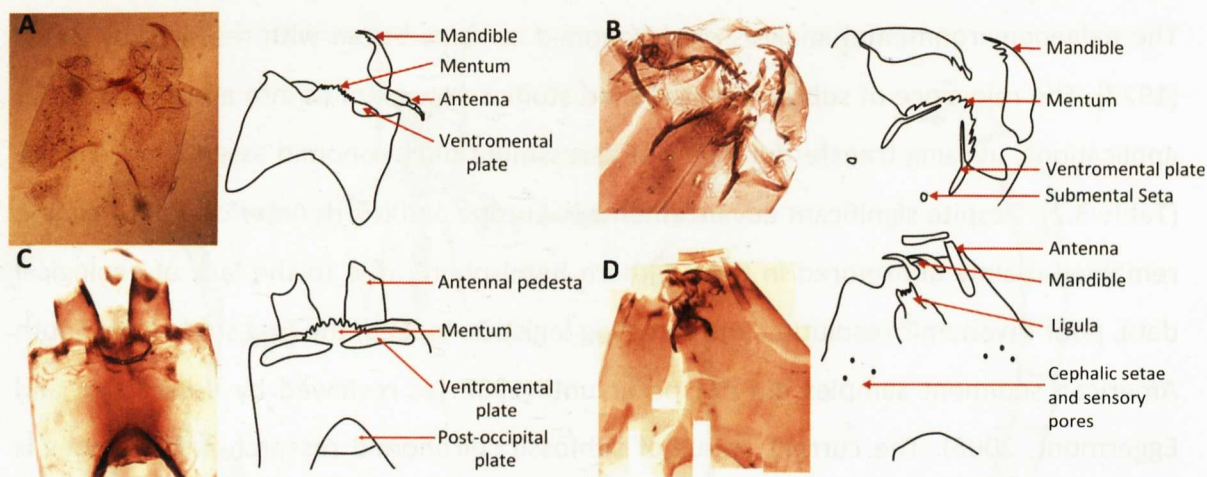
Although minimal in comparison to work from other regions, investigation of modern Neotropical distribution has progressed. Notably, the early contributions of Edwards (1931) from research in Patagonia, and the transantarctic relationships shown by Brundin (1966) were significant. The later inventories of Neotropical (Spies and Reiss, 1996) and, specifically, Andean Chironomidae (Roback and Coffman, 1983) have also been important steps in the developing the regional understanding. Examining the global distribution of chironomids, Ashe et al. (1987) reported 109 genera and 369 species from the Neotropics and twenty-one years later, Ferrington (2008) concluded taxon richness had increased to 154 genera and 618 species. This increase of described species and genera represents the greatest increase of any region. Although due to improved taxonomic classification and research, the impact of increased exploration and research of South American freshwater habitats may also be a cause of the described richness.



The palaeoenvironmental analysis of chironomid remains began with research by Gams (1927). The relevance of subfossil chironomid studies now extends into a broad range of applications, utilising transfer functions or assessment of chironomid assemblage change (Table 3.2). Despite significant advancements in Europe and North America, the discipline remained mainly unexplored in the southern hemisphere, due to the lack of ecological data, poor taxonomic resolution and sampling logistics. Indeed, the first study from South American sediment samples did not occur until 1982 (as reviewed by Verschuren and Eggermont, 2006). The current status of subfossil chironomid research in the Andes is discussed in Chapter 6.

Application	Sources
Anthropogenic land disturbance and pollution	(Kansanen, 1985; Woodward and Shulmeister, 2005)
Geological activity	(Araneda et al., 2007)
Hydrology (water depth)	(Hofmann, 1998)
Isotopic composition related applications ( $\delta^{18}\text{O}$ , $\delta^{13}\text{C}$ )	(van Hardenbroek et al., 2010; Verbruggen et al., 2010)
Lake pH levels	(Brodin and Gransberg, 1993; Johnson et al., 1990)
Lake trophic status (nutrient concentration, productivity etc...)	(Brooks et al., 2001; Gathorne-Hardy et al., 2007)
Oxygen regime	(Quinlan and Smol, 2001)
Salinity	(Chen et al., 2009; Walker et al., 1995)
Substrate / sedimentation type and input rate	(Schakau, 1991; Verschuren et al., 2000)
Temperatures (water and air)	(Brooks and Birks, 2001; Lang et al., 2010; Porinchu et al., 2003; Walker et al., 1991)

**Table 3.2** Example applications of palaeo chironomid studies together with select, non-exhaustive, reference list. List compiled, in part, with examples referenced by Brooks (2000), Nyman (2007), Verschuren and Eggermont (2006) and Walker (2001). Note: several of these applications are interlinked (water depth – salinity – temperature, sedimentation – human influence, etc...) and so some studies referenced encompass a range of applications.



**Figure 3.8** Morphology of chironomid larvae head capsules. Highlighted are a number of structures and characteristics that are commonly used to separate chironomid taxa. **A)** *Parachironomus* type. **B)** Orthocladinae type. **C)** *Tanytarsini* type. **D)** Tanypodinae type. Pictures are from specimens identified in this study.

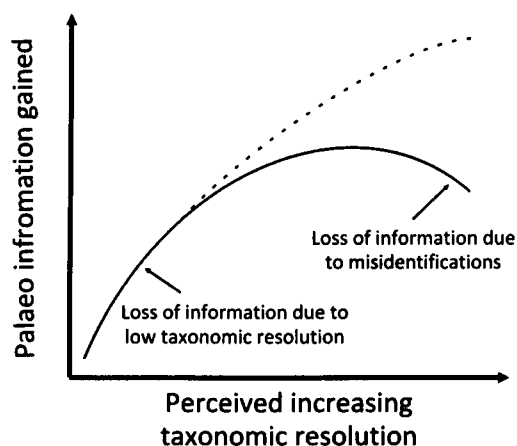
### Methodology

Subfossil chironomid analysis was conducted on subsamples of 1 cm<sup>3</sup> at an original resolution of 20 cm that coincided, where possible, with pollen and charcoal analysis samples. Sampling resolution was then refined by sampling specific depths where initial results indicated important shifts. Following an adapted version of the procedure described by Brooks, Langdon and Heiri (2007), samples were deflocculated in 10% (KOH), heated in water and sieved and separated into two size fractions of 90–212 µm and >212 µm. Head capsules were picked by hand from a sorting tray under a binocular microscope (Olympus SZX12) at ×12.5 to ×25 magnifications and progressively dehydrated. Depending on size and fragmentation of head capsules, between 1–5 were mounted ventral side up in Euparal mountant under 6 mm diameter coverslips onto a microscope slide. Identification was subsequently achieved using a Nikon Eclipse 50i microscope at ×400 magnification with reference to relevant keys (Brooks et al., 2007; Dieffenbacher-Krall et al., 2008; Epler, 1995; Epler, 2001; Rieradevall and Brooks, 2001; Wiederholm, 1983). Results were recorded on pre-designed recording sheets prior to digital data entry (Figure A2.3). The full preparation protocol is provided in Appendix A2.6.

### *Limitations*

As with palynology, there are various assumptions for subfossil chironomid analysis. These focus around the stability of environmental – ecological interactions through time, differential rates of preservation and contamination, and taxonomic resolution (see Section 3.4.1). Of all, the biggest prerequisite for meaningful palaeoenvironmental interpretation is consistent and proficient identification (Brodersen, 2008). Although new and well constructed taxonomic keys (e.g. Brooks et al., 2007; Dieffenbacher-Krall et al., 2008), together with advancements in microscope image capturing and comparison continue to help reduce this problematic issue, the damaging effects of misidentification remain high. Researchers are therefore still wary of over-confident nomenclature and are encouraged to adopt conventions to indicate certainty in identifications, as with pollen analysis (Walker, 2001). However, reluctance in refining identification to higher resolution may actually assist with the palaeoenvironmental information gained due to increased resolution often leading to increased errors (misidentification), an idea conceptualized by Walker (2001) (Figure 3.9), and later, in reference to specific outcome of correct and incorrect type separation, by Brodersen (2008) (Figure 3.10).

Recent statistical analysis supports a conclusion that transfer functions based upon the highest level of taxonomic (fine) resolution provide inference models with greater agreement to the modern measurements than those with low (coarse) resolution (Heiri and Lotter, 2010). However, this work also showed that intermediate taxonomic resolution produced very similar results to models based on the finest taxonomic data. In conclusion, it is apparent that the effect of increasing taxonomic resolution is dependent upon the analyst's expertise. As a result, an experienced analyst is less likely to suffer from the problems identified by Brodersen (2008), and obtain more palaeoenvironmental information when refining the taxonomic resolution (Figure 3.9, dashed line). For a less experienced analyst, attempts to refine the taxonomy are more likely to result in increased misidentifications (see Heiri and Lotter, 2010). Overall, the effect of different taxonomic resolution on environmental reconstructions does warrant continued investigation.

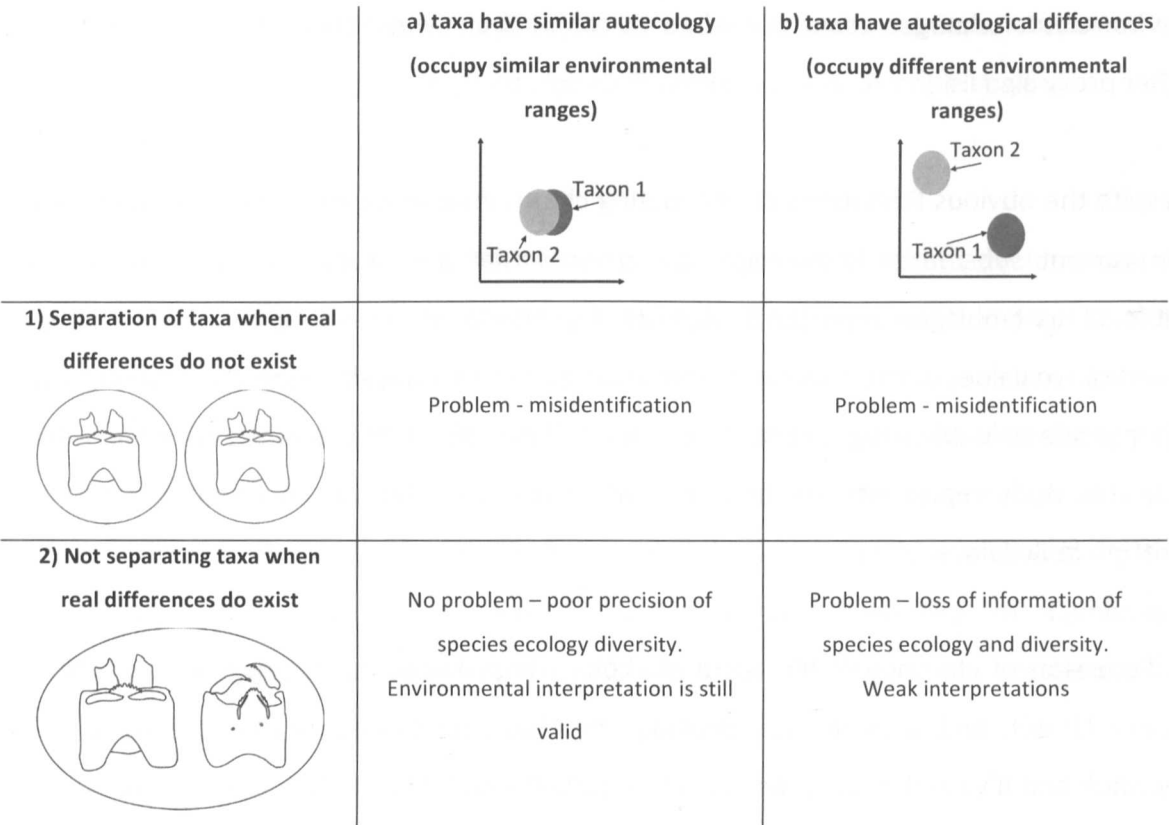


**Figure 3.9** Conceptual model representing the correlation between taxonomic resolution and palaeoenvironmental information gained during a study. An offset exists between the apparent (dashed line) and actual (solid line) information gained with perceived increasing taxonomic resolution. The ideal (optimum) situation is achieved just before misidentifications occur. Modified from Walker (2001) and with the later additions of Velle et al. (2010).

Other questions surrounding subfossil chironomid analysis that have attracted discussion include; i) the number (of head capsules) needed to be identified before a representative sample is recorded (Heiri and Lotter, 2001; Larocque, 2001), an issue encountered across palaeolimnology (e.g. Lytle and Wahl, 2005; Payne and Mitchell, 2009), and ii) with chironomid head capsules prone to splitting in some taxa more than others (*i.e.* Orthoclaadiinae), how should counts of different head capsule fragments be handled (see Walker, 1987)? These topics are discussed with reference to this study in Chapter 6, with the results of half vs. whole counts of split head capsules shown in Figures 6.4A and 6.5A.

The immaturity of both modern and subfossil chironomid analysis in South America, as previously highlighted, leads to an additional set of problems. There are currently no taxonomic keys to South American larvae and the underdeveloped knowledge of chironomids in all life stages throughout the continent generally inhibits high taxonomic resolution. The most significant progress in palaeoenvironmental reconstruction has been made in southern Chile and Argentina (Verschuren and Eggermont, 2006). Recent studies have highlighted improvements possible in resolving taxonomic difficulties when a research focus exists (Donato et al., 2008; Massaferrero et al., 2005; Massaferrero and Brooks, 2002; Massaferrero et al., 2009). However, this situation is a rarity and the high Andes (Bolivia/Peru) remains deficient in studies.





**Figure 3.10** Consequences of two types of taxonomic error in association to taxa that a) occupy similar environmental ranges, and b) occupy different environmental ranges. Separation of taxa incorrectly always results in problems while reluctance to define identifications to higher resolution produces fewer problems. Modified from Brodersen (2008). While during analysis it may be advised to split rather than lump, it is crucial that prior to any interpretation or numerical analysis that any splitting is reassessed.

A phenomenon that may assist with the identification of taxa from within high Andean sediments is the apparent hump-shaped relationship with taxon richness and elevation, with low richness at the extremes (Bigler et al., 2006; Nyman et al., 2005). While Andean high elevation lake environments do pose a significant challenge to living organisms, active chironomids have already been observed on glacial ice, -16°C at 5600 m above sea level in the Himalayas (Kohshima, 1984). Therefore the presence of chironomids in Andean sediments is expected.

At present, no data training set exists for the central/high Andean region. As a result, analysis of chironomids from lake sediments can only yield qualitative results, focusing on shifts with reference to current knowledge about the ecology of the taxa involved. However, any shifts fine or large scale, are still valuable indicators of lake or

environmental changes especially when in conjunction with either shifts or stability in other proxy signals.

Despite the obvious limitations of conducting chironomid research in the Bolivian Andes, the current substantial knowledge gap ensures that any study into modern and/or subfossil assemblages represents significant progress in the discipline. Even though quantitative values in changes cannot be assigned in this study, information gathered can still provide valuable insight regarding several, if not all, of the variables listed in Table 3.2. This study represents the first account of subfossil chironomid remains from any location in Bolivia.

A discussion of chironomid biology and ecology is provided by Armitage et al. (1995), Pinder (1986), and uses in palaeoecology by Hofmann (1988), Walker (1987; 2001), Il'yashuk and Il'yashuk (2004), Brooks et al. (2007) and Velle et al. (2010). In addition, a review of southern hemisphere Quaternary reconstructions is also available (Verschuren and Eggermont, 2006).

### ***3.5) Chronological framework***

With no other records from the region to compare the Challacaba and Khomer Kocha Upper core stratigraphy to, the extraction of material for radiometric dating presented the most suitable methodology from which to obtain an age control. As there was good indication that neither site would pre-date the last glacial maximum (LGM, c. 21,000 cal y BP) due to lake size and elevation, radiocarbon dating ( $^{14}\text{C}$ ) was selected. All dates were obtained via the Radiocarbon Facility (Environment) administered by the Natural Environment Research Council (NERC). All chemical pre-treatment was conducted at the facility prior to conversion to carbon dioxide and a graphite target, followed by accelerator mass spectrometer (AMS) analysis (<http://www.gla.ac.uk/nercrl/>). Two rounds of funding were awarded by NERC after peer-reviewed consideration by the NERC Radiocarbon Facility-Steering Committee (RCF-SC), one rangefinder (1287.0408/2008) and one standard 1463.0410/2010) application. Calibrated dates are given in Chapters 4



and 5 with full radiocarbon analysis results and preparation protocol reported in Appendix A3.1. The extraction methods for each sample type is described below.

#### *Macrofossil plant remains*

Following core splitting, any macrofossils visible on the split surface were immediately extracted using forceps and wrapped in foil packages. Samples were then dried at 40°C, weighed and the foil packages were placed within cleaned centrifuge tubes. Samples were sent to the NERC Radiocarbon Facility via overnight courier to keep the length of time and less ideal temperatures to a minimum. The laboratory set up and methods used for radiocarbon sample extraction and storage follows protocols established by the Quaternary Palaeoenvironments Group (QPG) at the University of Cambridge (<http://www.qpg.geog.cam.ac.uk/resources/14cprotocol/>) and guidance received from the NERC Radiocarbon Facility (pers. coms. P. Gulliver).

#### *Lake sediments (gyttja)*

Where no obvious macrofossils were available bulk sediment samples were taken for analysis. These were extracted using cleaned metal spatulas and placed within foil packages and centrifuge tubes as above. No drying of bulk sediments was conducted as per the guidelines of the analysing laboratory.

#### *Macroscopic charcoal and seed cases*

Following the calibration of the rangefinder dates achieved by extraction of the above two sample types, an offset between macrofossil and lake sediment samples became apparent (see Chapter 4 for discussion). With a lack of further macrofossil plant remains to date, refinement of the chronological control was established by the separation of macroscopic charcoal particles (and additionally discovered seed cases) from the lake sediment samples. Large particles of charcoal were extracted due to their relative ease of picking, and that they are considered to become trapped within lake sediments with a few years of the fire event (Whitlock and Larsen, 2001). Sampling depths were chosen based upon the requirement to pinpoint the timings of key environmental changes already highlighted by multi-proxy analysis, but also upon the available abundances of charcoal particles at those depths. Core subsamples (6–10 cm<sup>3</sup>) were heated in distilled

water for 10 minutes at 50°C, sieved into two size fractions to aid picking (100–179 and >180 µm), and material transferred to a Petri dish. Fine forceps were used to selectively pick particles of charcoal, seed cases and other plant material which were separated into vials and dried at 40°C overnight to establish dry weights. Samples were then transferred to the NERC Radiocarbon Facility as previously described.

### ***3.6) Analysis of geochemical and physical properties***

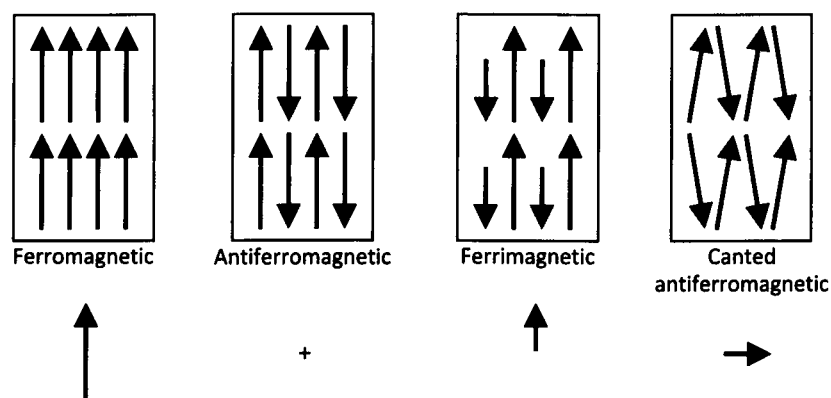
For all elemental, magnetic susceptibility and spectral analysis, subsamples of the sediment cores were taken every 5 cm, dried at 30°C and ground to a fine-grained powder with an agate mortar and pestle.

#### ***3.6.1 Magnetic susceptibility***

##### *Rationale for use*

The content and composition of magnetic minerals in lake sediments varies in association with the processes of weathering and erosion (Nowaczyk, 2001). These processes fluctuate in response to changes in climatic variability and human activity. As a result, determination of the mineral type and concentration offers a potential valuable source of information (Sandgren and Snowball, 2001).

All objects are magnetic and are affected by a magnetic field. Magnetism is based upon the relative mineral composition of the matter, and therefore can be described by magnetic properties (Dearing, 1994). The type of magnetic behaviour of a mineral is defined by the configuration and interactions of electrons, which orbit around the nucleus of an atom whilst individually spinning about their own axes of rotation (Dearing, 1994; Sandgren and Snowball, 2001). Several types of magnetic behaviour exist including ferromagnetism, ferrimagnetism, anti-ferromagnetism, canted anti-ferromagnets, paramagnetism and diamagnetism. The overall magnetic susceptibility of a material is therefore determined by the sum of all these types. Figure 3.11 summarises the distribution of magnetic vectors within some of the types, and a detailed description of each can be found in Sandgren and Snowball (2001), and Dearing (1994).



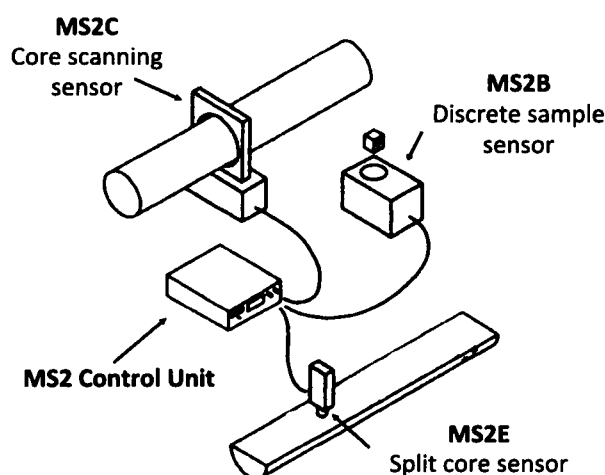
**Figure 3.11** Conceptual diagram of four types of magnetic behaviour. Arrow underneath each schematic demonstrates the net magnetism. Modified from Sandgren and Snowball (2001) and after McElhinny (1973).

Magnetic susceptibility is a measure of how readily a material can be magnetised (Thompson and Oldfield, 1986). It is a simple and common method by which the relative changes in the mineral composition of a sediment can be assessed. For instance, clay minerals are paramagnetic and will give higher magnetic susceptibility values than sediments composed of carbonates. The measuring process involves subjecting the sample to a low magnetic field, which in turn induces magnetisation of the sample material. The initial magnetic susceptibility recorded is a factor of the magnetic field externally applied ( $H$ ) and the magnetisation induced in the sample ( $M$ ). It is defined per unit volume of material and is therefore called magnetic volume susceptibility ( $\kappa$ ).

$$\kappa = M / H \tag{3.1}$$

Logging of magnetic susceptibility offers a valuable source of information that can be applied to almost any environmental research, acting as proxy indicator for changes in palaeoenvironmentally controlled depositional processes (Blum, 1997; Dearing, 1994). It is a non-destructive and fast process that is applied routinely to the majority of marine and lacustrine sediment cores, often at sufficiently high resolution to enable core-to-core correlation. Modern magnetic susceptibility measuring systems are capable of analysing sediment via a variety of different methods and can be performed on sealed cores, split

core sections or on discrete subsamples using the sensor designed for each purpose. Interchangeable sensors are available and should be selected based upon the material to be examined and the limitations of each sensor. One such popular system is the Bartington MS2 (Figure 3.12).



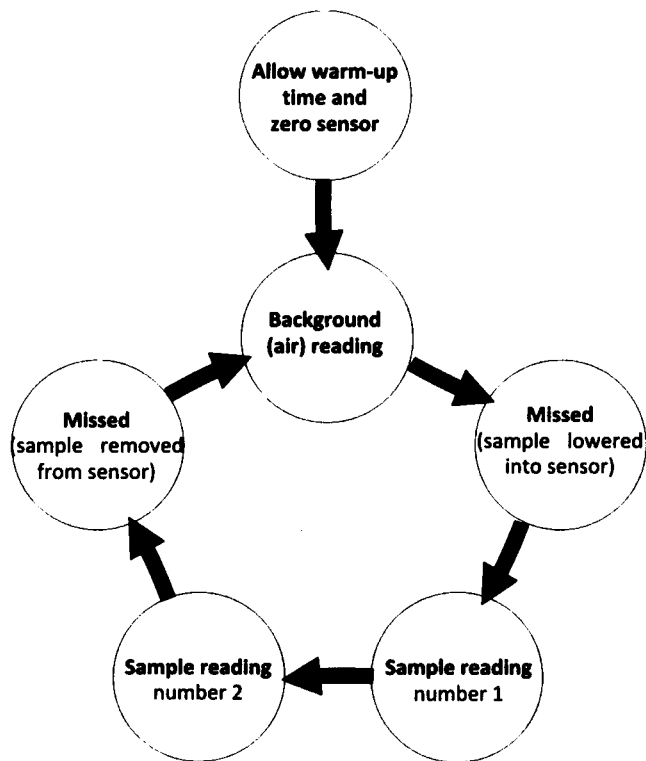
**Figure 3.12** Sketch of the Bartington MS2 Susceptibility System showing several of the interchangeable sensors available, including the MS2B used in this study. It should be noted that only one sensor can be attached at any one time. Diagram redrawn and modified from Nowaczyk (2001). For a full list of sensor types and uses see Dearing (1994).

### *Methodology*

All magnetic susceptibility readings were established using a Bartington MS2 Susceptibility System (Figure 3.12). Due to the sediment cores being contained within aluminium tubes, which upon investigation proved to be non-uniform in magnetic mineral composition, magnetic susceptibility measurements were performed on discrete subsamples of each core using the Dual Frequency Sensor (MS2B). The discrete subsampling method is the only methodology that allows for samples near the sediment/water interface to be measured. These samples have very high water contents and so typically do not remain contained during the long core procedure. Instead samples of this nature are obtained separately using a short core and are extruded into sample bags in the field (Sections 3.2.3 and Figure 3.1).

Analysis was conducted on a working surface made from stacked plastic crates positioned in the centre of large laboratory away from metallic objects. The laboratory’s relatively cool and constant temperature also made it a preferred location. Before measurements began, the Bartington sensor system was switched on to equilibrate and all samples were allowed to adjust to room temperature (~30 minutes). Height adjustment of the platform within the MS2B sensor, as detailed by Dearing (1994), was made using a homogenous mixture of sand to locate the point where the highest reading was obtained.

Following the protocol established by Dearing (1994), measurement was conducted continuously on all samples in one session. On continuous sampling mode, readings are displayed every ~10 seconds. For each sample two measurements were taken, between background (air) measurements, with missed/void readings occurring with sample insertion and removal (Figure 3.13). Readings were obtained from the MS2 control unit display set to standard international (SI) with a scale of  $10^{-5}$ . A range multiplier of 0.1 was determined with the MS2B sensor set to the high frequency (HF) range.



**Figure 3.13** Simplified measurement procedure using the Bartington MS2 Susceptibility System with the Dual Frequency Sensor (MS2B).

Initial magnetic susceptibility is defined per unit material and is called volume susceptibility ( $\kappa$ ). Readings were then corrected first for drift in the background (air) reading (Equation 3.2), and then for variation in mass differences and a mass specific susceptibility value ( $\chi$ ) determined (Equation 3.3). No correction for water content was required as the samples were dried prior to analysis.

$$\kappa \text{ (corrected)} = \text{sample } \kappa - [(\text{first air } \kappa + \text{second air } \kappa)/2] \quad (3.2)$$

$$\chi = \kappa \text{ (corrected)}/\text{dry sample weight} \quad (3.3)$$

### *Limitations*

The majority of limitations associated with recording magnetic susceptibility are connected with the sensor type and measurement protocol used. Nowaczyk (2001) demonstrated the physical limitation of several of the Bartington MS2 sensors and concluded that while the highest sampling resolution can be attained by the logging of a split core, measurements of discrete samples provide the greatest amplitude resolution. Many issues can also be minimised if well tested protocols are followed. Of particular importance is temperature stability during measurement and the need for standard sampling procedure/size. When attempts are made to quantify the results in terms of mineral composition determination, calibration issues increase substantially. In this study magnetic susceptibility is only used on a lake basin specific basis to examine changes identified within each core and measurements are only used in a qualitative sense.

Magnetic susceptibility remains a quick, inexpensive and non-destructive method by which to compliment the multi-proxy study of lake sediments. As a result it often provides the first data obtained from a new sediment core and can inform the researcher on overlapping core correlation, atypical depositional rates and gaps in accumulation (Thompson et al., 1975). However, there are situations where variations in magnetism of sediments may be influenced by diagenetic effects which need to be considered during any interpretation (Oldfield, 1991).



### 3.6.2 Spectral / Colour

#### *Rationale for use*

Colour logging is considered a useful and descriptive tool for assessing soil and sediment core composition (Rogerson et al., 2006). Today, it is routinely applied during the initial stage of core cataloguing using systems such as the Munsell Soil Color Chart, as demonstrated by this study (Section 3.3). However, this methodology of colour description still remains to some degree subjective and only produces descriptive results of the sedimentology. Digital spectral analysis provides a technique for the quantification of colour variations observed. Like magnetic susceptibility, it offers a rapid, inexpensive and non-destructive approach for logging many types of stratigraphic successions, including geologic strata and lake or marine sediments (Nederbragt and Thurow, 2005; Rogerson et al., 2006). Once complete, results can then often be associated with a range of controls including regularly occurring phenomena (e.g. ENSO), longer-term cyclic events (e.g. Milankovich orbital cycles) or just gradual changes in sediment composition (e.g. deglaciation). In sediment cores, total organic carbon, carbonate, iron and clay content have been found to be some of the possible controls of sediment colour (Nederbragt et al., 2006; Rogerson et al., 2006).

The predominant numerical system used to describe colour is defined by the Commission International de l'Eclairage (CIE) by the  $L^* a^* b^*$  system which allows lightness ( $L^*$ ) and chroma ( $a^*$ ,  $b^*$ ) to be quantified. However, the common method by which colour data is collected digitally is by measuring the intensities of the red (R), green (G) and blue (B) colour channels. In the RGB system, values range from 0–255 in each channel with pure white defined as 255,255,255 and black as 0,0,0. The RGB recording method is the most common in digital cameras/scanners and is now one of the primary outputs of image analysis software. From the examination of lake sediment cores, it has also been found that some colour channels exhibit significantly higher variance than the others due to site specific conditions (e.g. Moy et al., 2002). As a result colour channel data can be analysed individually to obtain the maximum amount of information possible.

The most essential part to any image analysis, including colour, is the primary step of image acquisition (Nederbragt and Thurow, 2005; Saarinen and Petterson, 2001). For lake

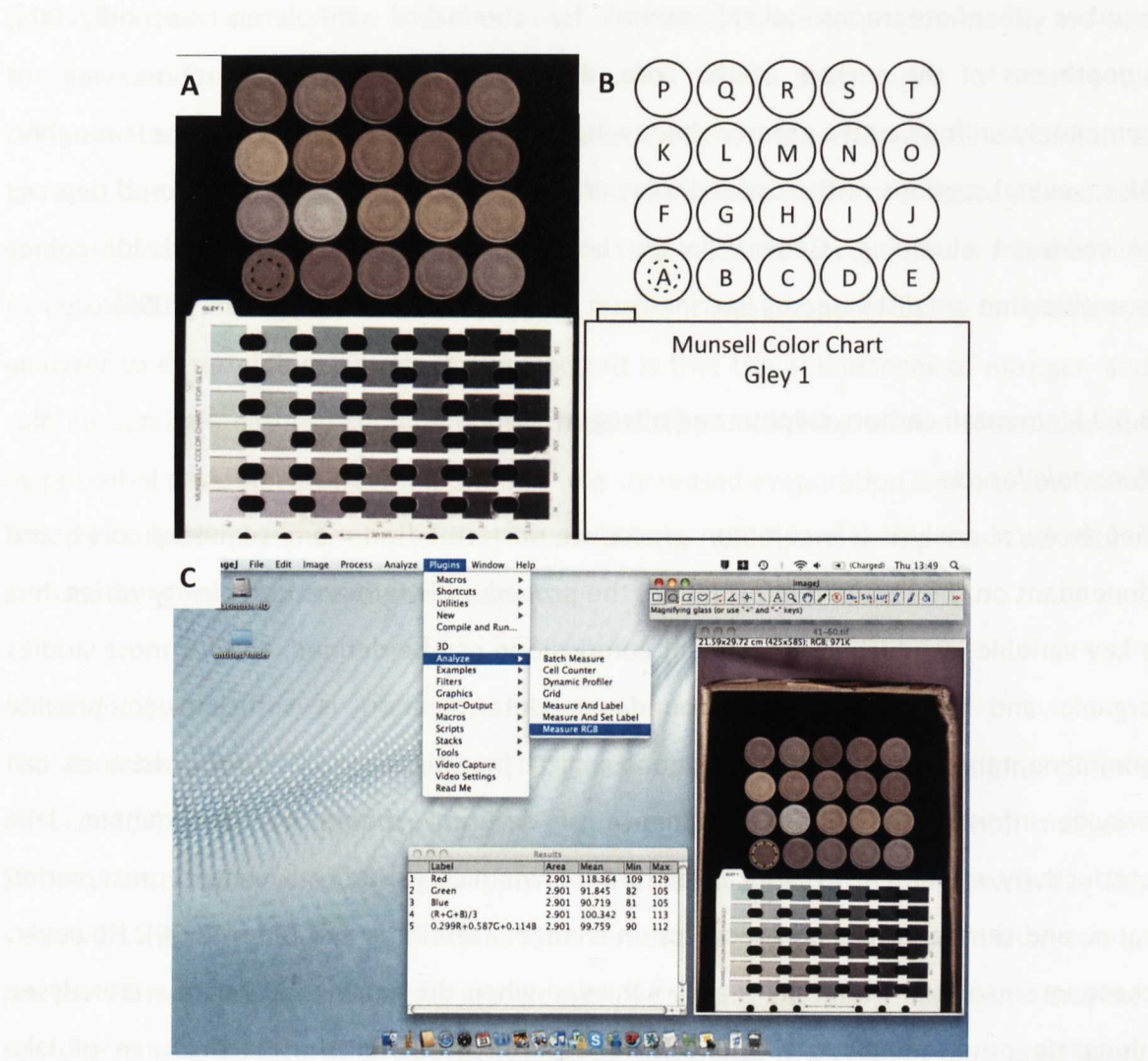
and marine sediments this is commonly achieved using a multifunction instrument such as Itrax Corescanner system which produces detailed colour images as well as performing simultaneous elemental x-ray fluorescence analysis and magnetic susceptibility. However, as described previously (Section 3.3.2), other methods of obtaining images of a sediment core surfaces exist. Due to the limitations of the core photographing procedure undertaken during this study, and the observation that only small sections of the cores obtained show lamination, image analysis for this study was conducted upon discrete, dried samples of sediment already extracted from the core for the purpose of elemental analysis. This avoided the effects of darkening or glare caused by wet sediments, but at the expense of a higher resolution.

### *Methodology*

Colour properties of discrete samples were analyzed using a Canon LiDE30 flatbed scanner, which uses LED (light emitting diode) illumination. The uniformity of illumination was tested by scanning a sheet of pure white paper and no deviation in colour was found across the scanning surface. Clear sample vials were positioned directly onto the scanning surface and ambient light excluded using a blacked-out box which covered the scanning unit. Each sample was scanned in two different locations on the scanning surface 10 spaces apart (Figure 3.14A and B). Prior to scanning, each sample vial and the glass of scanning surface was cleaned thoroughly to remove any fingerprints, dust or other marks. The sediment in each vial was agitated until the whole of the vial base was uniformly covered in sediment.

Scanning was performed at the highest resolution possible (611 dpi) and imported into Corel Draw Graphic Suite. Files were then saved as a windows bitmap image (.bmp) file to maintain as high resolution as possible (~100 mb per file) and imported into ImageJ. Using the standard tools available in ImageJ, a standard elliptical section from the central portion of each scanned vial was individually selected for analysis, being careful to avoid blemishes on the sample vials or voids where the sediment quantity was low (Figure 3.14C). The area selected on each vial image corresponded to a circular area of ~15 mm in diameter. This resulted in the RGB colour channels recorded being an average of >145,000 individual pixels values. Averaging pixel values from across an area of this size

minimises the effects of any non-uniform colour distribution across the sample. Data was copied into an Excel spreadsheet files for future handling alongside other proxy data.



**Figure 3.14 A and B)** Scanning procedure layout. **C)** Screenshot of colour analysis using ImageJ. For each sample, only the central section (as identified by dashed line) is selected for colour analysis.

### Limitations

As already discussed, the critical requirement, and therefore major limitation, of colour analysis is image acquisition. As a result of the protocol undertaken for this study, the sampling resolution was not high enough to detect any laminations in the core, which requires detailed continuous core photographs. While the photographic procedure outline in Section 3.3, produced results that upon visual inspection appear to accurately represent the core surface, there are several issues with the cores that would severely

impact on the production of a high resolution colour image. Firstly, pooling of water on the surface of the core introduces glare which, while can be reduced by increasing the number of photographs taken, cannot be eliminated completely. Secondly, the smoothness of the surface of the core, due to the sediment composition, was not completely uniform and a greater shadowing effect occurs where the surface is rougher. Also, several sections of the cores display cracking while other sections suffered degrees of sediment slumping. General image analysis techniques and methods of colour quantification are discussed by Saarinen and Petterson (2001) and Francus (2005).

### **3.6.3 Elemental: carbon, sulphur and nitrogen**

#### *Rationale for use*

Geochemical analysis is a common procedure performed on many sediment cores, and dependant on the required information, the procedure length and complexity varies. It is a key variable by which lake sediment composition can be defined, and for most studies organic and inorganic carbon abundance determination is sufficient to provide complimentary data for many palaeoecological investigations. The data obtained can provide information on the dominance of different processes; for example, lake productivity, mineral inwash, local vegetation dynamics, glacial re-advances, preservation rates, and temperature and precipitation changes (see Birks and Birks, 2006). However, these interpretations are only readily achieved when the geochemical data are analysed alongside other multi-proxy findings. In most instances, the primary source of lake sediment organic matter is from plants situated in, or in close proximity to, the lake site (Meyers and Teranes, 2001). This understanding has important implications for the interpretation of the spatial scales represented in a sediment core.

Baker et al. (2001) identified calcium carbonate ( $\text{CaCO}_3$ ) as a potential indicator of low lake level as it is affected by both water depth and salinity. Precipitation of  $\text{CaCO}_3$  occurs because of decreased solubility with the decreased pressure, decreased partial pressure of  $\text{CO}_2$  ( $p\text{CO}_2$ ) and increased temperature, together with an associated salinity increase due low water level.  $\text{CaCO}_3$  concentrations have already been used in several Andean environments to indicate periods of reduced lake level (Cross et al., 2000; Hillyer et al., 2009).

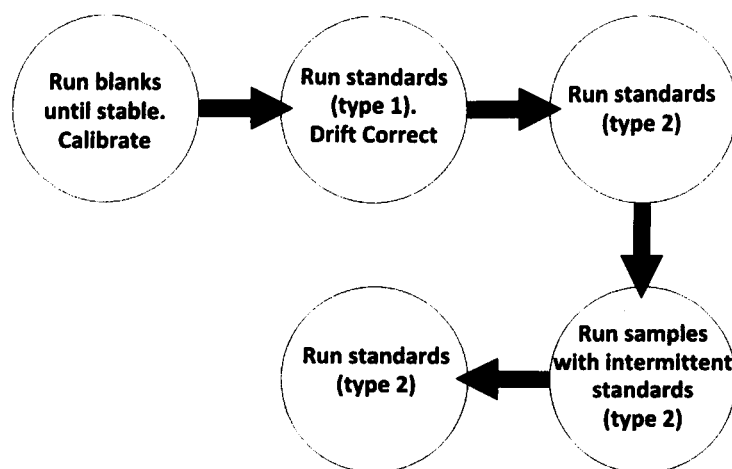
The amount of organic and carbonate contents in sediments can be measured via the sequential loss on ignition (LOI), or by the use of geochemical instruments. Heiri et al. (2001) discussed some of the limitations that surround LOI, which predominantly are due to non-standardised laboratory protocols. The main advantages of elemental determinator instruments are that the combustion and measurement of all carbon is ensured due to temperatures in excess of 1350°C, that the protocol is standardised and comparable results between labs, and that the time taken to run samples is minimal due to autoloading devices (Schumacher, 2002). Another advantage of using an elemental analyser to determine sediment carbon content is that the abundances of nitrogen and sulphur can be measured simultaneously. Previously studies have shown that these can be potential palaeoenvironment indicators (e.g. increased evaporation and lake low stand linked to sulphur (Brenner et al., 2002; Fritz and Saros, 2006), and so represent additional information gained at no extra time expense.

### *Methodology*

The abundance (wt%) of total carbon (TC), total inorganic carbon (TIC), sulphur (S) and nitrogen (N) was determined using the in-house LECO CNS-2000 elemental analyzer. Sample runs were achieved using weights of 0.2 g for TC, S and N measurements. For TIC, values 0.15 g were first “ashed” at 450°C to remove all organic carbon and then run as per the TC measurement. Samples are measured only after stability is achieved and the instrument is calibrated using known standards. Intermittent standards measured every 10 samples allows for any long-term drift to be assessed and 80 samples can routinely be measured in one day (Figure 3.15). See Appendix A2.7 for a detailed analytical protocol. Total organic carbon (TOC) and calcium carbonate (CaCO<sub>3</sub>), are calculated by the following (Equation 3.4 and 3.5):

$$\text{TOC} = \text{TC} - \text{TIC} \quad 3.4$$

$$\text{CaCO}_3 = \text{TIC} * 8.33 \quad 3.5$$



**Figure 3.15** Simplified measurement procedure using the LECO CNS-2000 elemental analyser.

### *Limitations*

Ultimately, determination of sediment elemental composition is a productive, yet easily achieved analytical technique. However, as noted by Shuman (2003), despite this simplicity, interpretation can be remarkably complex due to in-lake processes (Birks and Birks, 2006). As previously discussed, the advantages of analysis using instrumentation, such as the LECO determinator, over sequential LOI are significant. However, limitations associated to all sensitive instrumentation are cost (initial set up and ongoing consumables), and that stability must first be achieved prior to analysis. In particular to the LECO analyser, a leak free gas flow must be established otherwise atmospheric gases will increase the values obtained.

### **2.7) Statistical functions and software packages**

A range of software and statistical methods were utilised throughout the course of this study (Table 3.3). Where necessary (*i.e.* radiocarbon calibration, zonation and ordination), a rationale for the choice of method used is provided in the relevant data chapter. In many cases, the choice of software was limited to that currently available at The Open University, and it should be noted that other software packages will provide the necessary functions to the required standard. Discussion of the application of software to data sets and output in this research occurs in Chapters 4–6.



Function Technique	Software	Reference
Climate data overlay	ArcGis	
Data entry	Microsoft EXCEL	
Figure preparation and image overlays	Corel Graphics Suite 11 and 13	
File conversions	WinTran v1.4	(Juggins, 2002)
Microscope Digital Photography	ImageJ v1.41o	(Rasband, 1997-2009)
Ordination Non-metric multidimensional scaling (NMDS) Detrended Correspondance Analysis (DCA)	PC-ORD v5.0	(McCune and Mefford, 2006)
Radiocarbon date calibration	CALIB 6.0.1 (SHCal04 Southern Hemisphere data set) and Fairbanks Calibration Curve	(Fairbanks et al., 2005; McCormac et al., 2004; Stuiver and Reimer, 1993; 2010; Stuiver et al., 2005)
Spectral Analysis (Colour properties (RGB))	ImageJ v1.41o	(Rasband, 1997-2009)
Stratigraphic diagrams	C2 v1.4 (beta)	(Juggins, 2003)
Zonation (Optimal sum of squares partitioning)	ZONE v1.2	(Lotter and Juggins, 1991)
Zonation Significance Assesemnt (Broken-stick model)	BSTICK v1.0	(Line and Birks, 1996)

**Table 3.3** Software packages and functions applied in this study.

## **Chapter 4)**

### ***Four thousand years of environmental change and human activity in the Cochabamba Basin, Bolivia***

In this chapter, all fossil pollen, spore, charcoal, geochemical and geophysical data from the Lake Challacaba study site are presented and discussed. This chapter has been published separately:

**Williams, J.J., Gosling, W.D., Coe, A.L., Brooks, S.J. and Gulliver, P.** Four thousand years of environmental change and human activity in the Cochabamba Basin, Bolivia.

*Quaternary Research* (Online) DOI: 10.1016/j.yqres.2011.03.004

---

#### **4.1) Abstract**

The Cochabamba Basin (Bolivia) is on the ancient road network connecting Andean and lowland areas. Little is known about the longevity of this trade route or how people responded to past environmental changes. The eastern end of the Cochabamba valley system constricts at the Vacas Lake District, constraining the road network and providing an ideal location in which to examine past human–environmental interactions. Multi-proxy analysis of sediment from Lake Challacaba has allowed a c. 4000 year environmental history to be reconstructed. Fluctuations in drought tolerant pollen taxa and calcium carbonate indicate two periods of reduced moisture availability (c. 4000–3370 and c. 2190–1020 cal yr BP) compared to adjacent wetter episodes (c. 3370–2190 and c. 1020 cal yr BP–present). The moisture fluctuations broadly correlate to El Niño/Southern Oscillation variations reported elsewhere. High charcoal abundance from c. 4000 to 2000 years ago indicates continuous use of the ancient road network. A decline in charcoal and an increase in dung fungus (*Sporormiella*) c. 1340–1210 cal yr BP, suggests that cultural changes were a major factor in shaping the modern landscape. Despite undisputable impacts of human populations on the *Polylepis* woodlands today, we see no evidence of woodland clearance in the Challacaba record.

## 4.2) Introduction

The highly diverse ecosystems of the elevated tropical Andes are vulnerable to change from increasing human occupation of the area and predicted future climate change (Cincotta et al., 2000; Malcolm et al., 2006; Myers et al., 2000). To develop an effective policy to conserve and manage this ecosystem, a robust understanding of the region's natural history is required (Godwin, 1956; Willis and Birks, 2006). Today, uncultivated sections of the high Central Andes are principally grassland within which are pockets of woodland dominated by the tree genus *Polylepis* (Rosaceae). Kessler (2002) has implied that the relationship between grassland and woodland ecosystems is influenced strongly by human practices and an intensive landuse at high elevations has limited severely *Polylepis* woodland distribution today (Ellenberg, 1958; Fjelds  and Kessler, 1996). However, the nature and degree to which human factors ultimately govern the ecology of this region remains unclear and recent research has highlighted the vulnerability of these Andean woodlands solely to climatic lead changes (Gosling et al., 2009).

The main Cochabamba Basin (eastern Andes, Bolivia; Figure 4.1A) is, today, a major region for food production. The topography favors agriculture because it is: i) on an easily accessible trade route between upland and lowland areas and, ii) provides a flat area of land upon fertile Quaternary deposits, that largely experience a temperate seasonal climate. Limited archaeological evidence from the region suggests a long human history around Cochabamba with agricultural practices from at least 3000 years before the present (cal yr BP) (Hensen, 2002). By the time of the Tiwanaku state (c. 1500–900 cal yr BP), the warm fertile main Cochabamba Valley had become a center for farming, and frontier for trade into the subtropical Mizque Valley (Higueras, 1996; Janusek, 2008).

The collapse of the Tiwanaku state, around 1000–900 cal yr BP, has been linked to a prolonged drought on the Altiplano as indicated by the low water levels of Lake Titicaca (Abbott et al., 1997; Binford et al., 1997) and an elevated dust signal from the nearby Quelccaya (Peru) ice core record (Thompson et al., 1985). Elsewhere in the eastern Central Andes (*i.e.* Marcacocha), the impacts of human occupation on the landscape, identified from lake sediment records, are correlated to changes in agricultural practices, herbivore domestication and cultural adjustments over the last 4000 years (Chepstow-

Lusty et al., 1998; 2007). Regardless of whether climatic events were coupled with a social transformation (Janusek, 2008), the transition from Tiwanaku fragmentation and collapse (1000–900 cal yr BP), towards rule by the Inca Empire (c. 650–550 cal yr BP, 1400–1533 AD), is certain to have had major impacts on both societies and the landscapes of the Cochabamba valleys.

In this study, we present a continuous 4000 yr paleolimnological record from the Vacas Lake District in the Cochabamba Basin, using a multi-proxy approach to provide the first submillennial-scale reconstruction of vegetation, fire and cultural change from the Eastern Cordillera of the Bolivian Andes. These data provide new insights into the interaction between climate change, pre-Columbian societies and the environment.

#### **4.2.1) Regional setting**

The Vacas Lake District is a system of six lakes located within a cold (7.2–11.3°C), seasonally dry (2.6mm/month June–August, 114mm/month January–March), high elevation valley (Hijmans et al., 2005; Ritter, 2000). The district is situated east of the main Cochabamba Basin and north of the Mizque valley (Figure 4.1). Located within the Inter Andean/Eastern Cordillera forethrust zone (McQuarrie, 2002), the local geology is not known in detail, but the surrounding high ground consists of Ordovician quartzite and sandstone, with the Vacas valley, as with the main Cochabamba Basin, sitting on Quaternary sedimentary deposits (Cassard, 1999). Ritter (2000), has speculated that all six lakes within the Vacas municipality were once a single connected system.

Regional climate, predominantly precipitation, is controlled by a variety of systems including the movement of the Intertropical Convergence Zone (ITCZ) (Leduc et al., 2009), and the variability of the South American summer monsoon (SASM; Zhou and Lau, 1998). However, it is the El Niño-Southern Oscillation (ENSO) that is considered to be the largest source of inter-annual variation (Chiang, 2009; Philander, 1990).

The Vacas Lake District is positioned within the Central Andean Puna ecoregion (Olson et al., 2001), and specifically, within the “northern Puna-semi-humid” and “sub-humid Puna and Punean woodlands of the Tunari” biogeographic regions (Ibisch *et al.*, 2003; Navarro

and Maldonado, 2002). Vegetation types range from grassland, shrubland and woodland (Navarro and Ferreira, 2007). Important genera of these biogeographic regions, include: *Poa*, *Festuca*, *Deyeuxia*, *Muhlenbergia*, *Stipa* (Poaceae), *Gomphrena* (Amaranthaceae), *Baccharis* (Asteraceae), *Polylepis* (Rosaceae), *Peperomia* (Piperaceae), *Astragalus* (Fabaceae) and *Puya* (Bromeliaceae) (Navarro and Maldonado, 2002).

Today, the flatter land surrounding the Vacas lakes is dominated by the cultivation of potatoes and other tubers, and has also been heavily impacted by grazing (Gotkowitz, 2007). Further away from most harshly effected lands, and more typical of the Cordillera of Tiraque-Vacas, the landscape consists of *Polylepis* woodland patches within Andean grassland. Studies of *Polylepis besseri* woodlands at Sacha Loma (17°44' S, 65°34' W; 3800m elevation) have provided a detailed inventory of associated species (Fernández, 1997; Fernández, et al., 2001). The most local *Polylepis* woodland patches are located ~5 km away in the mountains to the northeast, and ~10 km to the southwest (Figure 4.1B). Our own observations of a *Polylepis nana* stand by the side of the Arani-Vacas road (17°33.540' S, 65°42.329' W; 3379 m asl), revealed tree heights of 1–1.5 m growing in patches along the edge of a rocky field boundary.

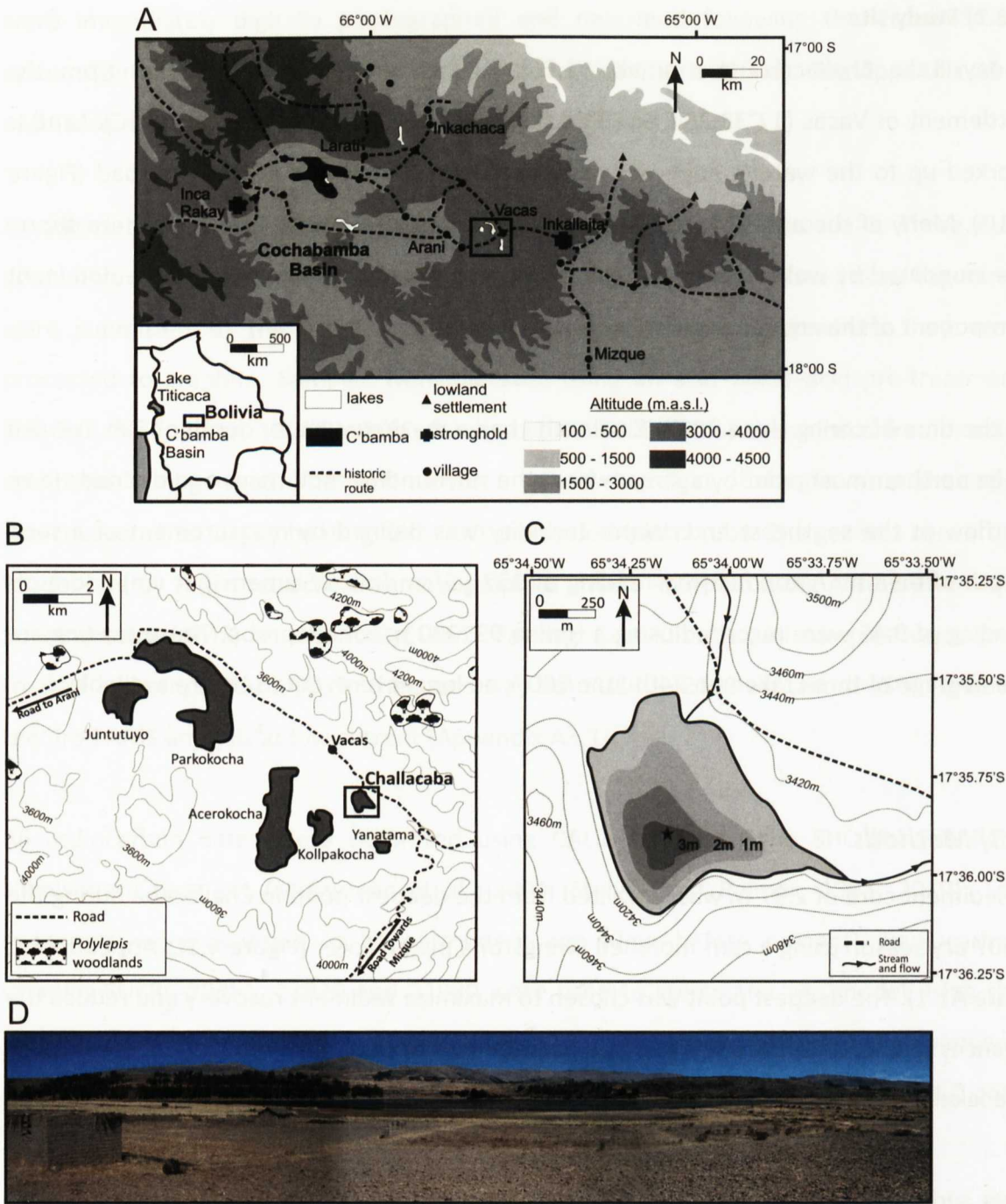
Surveys of the aquatic vegetation at Acerokocha, Juntutuyo, Kollpakocha and Parkokocha lakes (Figure 4.1B), highlighted the presence of *Lemna* (Lemnaceae), *Schoenoplectus* (Cyperaceae), *Myriophyllum* (Haloragaceae) and, *Zannichellia* and *Potamogeton* (Potamogetonaceae) (De la Barra, 2003; Molina et al., 2007). The Vacas lakes are regarded as an important source of water and feed (*Myriophyllum quitense*) for cattle which are driven into the lake during the dry season (Ritter, 2000).

Vacas is only ~15 km away from the well-documented Inca site of Inkallajta. Sánchez (2008) has suggested that the Vacas municipality was significant in regional transport routes (Figure 4.1A). Based upon the historical “high road”, the current road passing through the Vacas lakes was once a principle route linking the main Cochabamba Valley and the fuertes (strongholds) of Inca Rakay in the west, to those in the southeast such as Inkallajta and the Tiwanaku archaeological site of Mizque (Higueras, 1996) (Figure 4.1A). Given the importance of camelid pastoralism and caravans for pre-Columbian peoples

(Lynch, 1983) and the movement of Tiwanaku traders between the main valley and the Mizque enclave (Janusek, 2008), it seems likely that many groups of people would have had direct contact with the Vacas lakes.

Following preliminary investigation, Lake Challacaba was selected as the most suitable of the Vacas lakes for coring based upon its apparent permanence, relative freshwater content, suitable depth and accessibility. Our investigation into Parkokocha concluded that only 2 m of sediment would be recoverable from beneath 1.6–2 m of water, while Acerokocha proved too deep to core with the equipment available. The only previously published investigation recorded that Juntutuyo dried out for prolonged periods prior to 2300 yr BP (Abbott et al., 2003), despite at present having a maximum depth in excess of 3.5 m (Ritter, 2000).





**Figure 4.1** Maps showing study site location within Bolivia. **A)** Cochabamba Basin with altitudes, current city extent, other settlements and historic routes marked. Modified from Sánchez (2008). Inset map locates Cochabamba Basin within Bolivia. **B)** Vacas Lake District. The distribution of *Polylepis* woodlands as mapped by Fjeldsø and Kessler (1996) is shown. Contour lines at 200 m intervals. **C)** Lake Challababa (also known as Pilawitu). Bathymetry shown in metres. Contour lines at 20 m intervals. Coring location marked by star. **D)** Composite photograph of Lake Challababa looking south-west. Photographs taken June 2007. W.D.Gosling.

#### **4.2.2) Study site**

Today, Lake Challacaba is a small,  $\sim 1.5 \text{ km}^2$ , freshwater system, 2.5 km from the settlement of Vacas ( $17^\circ 33.257' \text{ S}$ ,  $65^\circ 34.024' \text{ W}$ ; 3400m elevation; Figure 4.1C). Land is worked up to the water's edge with associated small buildings nearer the road (Figure 4.1D). Many of the areas of worked land, especially those on the flatter northern shore, are inundated by water during the wetter months. *Myriophyllum* spp. was the dominant component of the aquatic vegetation.

At the time of coring (June 2007) Challacaba had a maximum water depth of 3 m. It is fed at its northernmost point by a stream from the surrounding mountains and drained via an outflow at the southeast end. Water turbidity was defined by measurement of a secchi depth of 0.58 m. A conductivity reading of  $332 \mu\text{S/cm}$  (microSiemens per cm) and a pH reading of 9.45 were recorded using a Hanna 991300 handheld probe. These reading are the average of three taken on 24th June 2007; no longer term data sets are available.

#### **4.3) Methods**

A sediment core of 2.97 m was extracted from the deepest point in Challacaba during the 2007 dry season using a cam-modified Livingstone piston corer (Figure 4.1C; Appendix A1; Plate A1.1). The deepest point was chosen to maximize sediment recovery and reduce the chances of encountering a sediment gap caused by any periods of reduced areal extent of the lake.

Two sediments cores (Challacaba-B and Challacaba-C) were recovered with staggered, overlapping, starting depths below the sediment–water interface (46 cm and 27 cm). The overlap ensured that a continuous record was recovered despite potential loss from some tube ends. Sediment cores were recovered in aluminum tubes (50 mm diameter, 1 m long) and sealed on site. The sediment–water interface and top 60 cm of sediment were recovered using a Perspex surface sample. The surface sampler was extruded in the field and continuous subsamples of 1 cm thickness bagged. All sediment recovered was transferred to The Open University cold store ( $4^\circ\text{C}$ ). The sediment cores were split and then sediment divided using a fine strand of wire held at tension. Once split, sediments

were immediately digitally photographed and described following the Troels-Smith system (Birks and Birks, 1980) and Munsell Soil Color Charts (2000). See Appendix A1.1 and Table A1.1 and A1.2 for description methodology and key.

A radiocarbon chronological framework was established for Challacaba-B. Three bulk gyttja, two macrofossil plant remains, and one set of picked charcoal/seed case fragments were submitted to the NERC Radiocarbon Facility (Environment) where they were processed to graphite. Samples were digested using an acid-alkali-acid pre-treatment (2M HCl, 80°C, 2 hrs; 1M KOH 80°C, 2 hrs; 1M HCl 80°C, 2 hrs) then rinsed free of acid, dried and homogenised. The total carbon in a known weight of the pre-treated sample was recovered as CO<sub>2</sub> by heating with CuO in a sealed quartz tube. The gas was converted to graphite by Fe/Zn reduction. Sample graphite's were analysed using Accelerator Mass Spectrometry (AMS) at the SUERC AMS Facility, East Kilbride. All samples were pre-treated and prepared to CO<sub>2</sub> in the same way but SUERC-32100 contained <500 µgC and required AMS analysis at low current (Appendix A3.1).

All radiocarbon dates were calibrated using CALIB 6.0.1 and the SHCal04 Southern Hemisphere data set (McCormac et al., 2004; Stuiver and Reimer, 1993; 2010). Top sediments were assumed to be of modern age (0 yr before present). Radiocarbon samples SUERC-22351, 21929 and 21930 were used to create the age model using the mean value of the largest probability at 2 sigma. Linear interpolations were used between dates and to extrapolate for the basal sediments. The chronology for Challacaba-C core was established by matching sediment units to Challacaba-B.

For physical and chemical analysis, samples were taken every 5 cm, dried for 7 days at 30°C and ground with an agate mortar and pestle. The magnetic susceptibility of each sample was measured using a Bartington Dual Frequency Sensor (MS2B), corrected for mass differences (Section 3.6.1). Color properties were analyzed using a Canon LiDe flatbed scanner and the software ImageJ (Rasband, 1997–2009). Separate readings for red (R), green (G) and blue (B) color intensities were recorded but after analysis, all three showed similar variance so a mean red, green and blue (RGB) value is used in this work (Section 3.6.2). The abundance of total organic carbon (TOC) and calcium carbonate

(CaCO<sub>3</sub>) was determined using a LECO CNS-2000 elemental analyzer (Section 3.6.3; Appendix A2.7).

Cores were subsampled (1 cm<sup>3</sup>) for pollen and fungal spore analysis and, after spiking with microspheres to allow for concentration calculation, chemical preparation followed standard palynological protocol (Faegri and Iversen, 1989; Appendix A2.4). Samples were mounted in glycerol and pollen was identified using a Nikon Eclipse 50i microscope at ×400 and ×1000 magnification. A minimum of 300 fossil terrestrial pollen grains were analyzed in each sample or, where concentration was extremely low, counting was continued until 3000 microspheres had been recorded. Percentage values for aquatic taxa (Lemnaceae *cf. Lemna*, Cyperaceae, *Isoëtes*, *Myriophyllum*, *Typha*), the spore group and the green algal genus *Pediastrum* were calculated relative to the pollen sum and their own abundance. Pollen grains and spores were identified using The Open University pollen reference collection, the Neotropical Pollen Database (Bush and Weng, 2006) and other pollen keys (Hooghiemstra, 1984; Roubik and Moreno, 1991). All pollen and spore types recorded were described and digitally photographed for reference purposes (Appendix A4: Enclosure CD1).

Charcoal analysis was conducted at the same sampling resolution as pollen. Subsamples of 1 cm<sup>3</sup> were deflocculated with 10% KOH for 24 hours before being sieved and separated into two size fractions; >180 µm and 100–179 µm (Appendix A2.5). Samples were then suspended in water on a gridded petri dish and counted using a binocular microscope (Olympus SZX12) at ×12.5 to 25 magnifications. A distinction was made between wood and herbaceous fragments based upon appearance. Charcoal is shown as particulates per cm<sup>3</sup> (counts/cm<sup>3</sup>).

All data sets were entered as EXCEL spreadsheet files with necessary conversions accomplished using WinTran V1.4 and diagrams plotted using the program C2 (Juggins, 2002; Juggins, 2003). Pollen zones were determined by optimal sum of squares partitioning (Birks and Gordon, 1985) performed using the software ZONE v. 1.2 (Lotter and Juggins, 1991). Assessment of zonal significance was subsequently completed using the broken-stick model (Bennett, 1996; Birks, 1998) in the software BSTICK v. 1.0 (Line

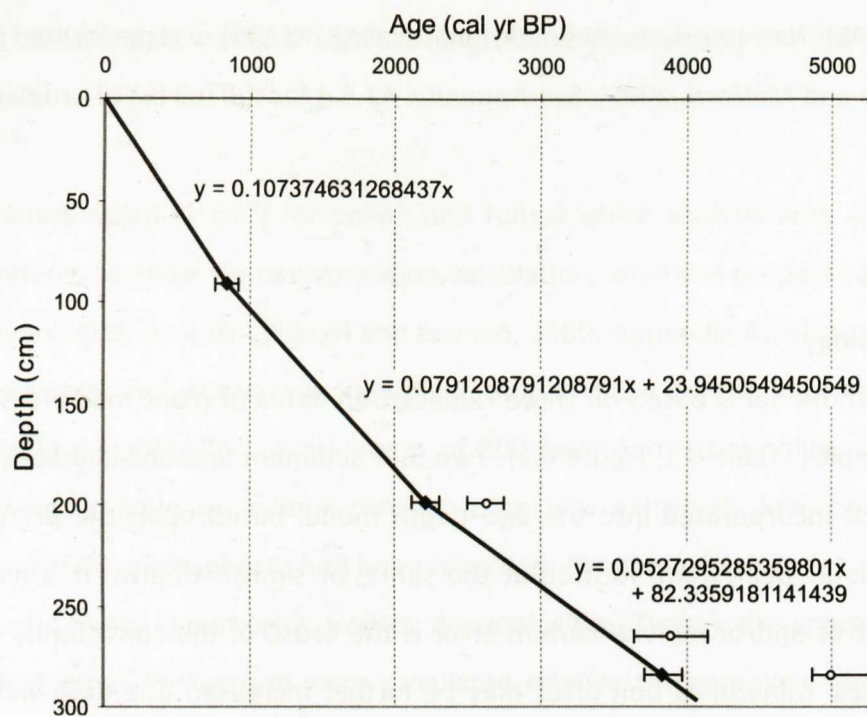
and Birks, 1996). Non-metric multidimensional scaling (NMDS) was performed in PC-ORD v5.0 (McCune and Mefford, 2006). See Appendix A3.3.4 for the full list of ordination data.

## **4.4) Results**

### **4.4.1) Chronology**

The age–depth model is based on three radiocarbon dates of plant macrofossils or bulk sediment samples (Table 4.1, Figure 4.2). Two bulk sediment and one charcoal/seed case date were not incorporated into the age–depth model based upon the preference for macrofossil dates (leaf/stem) located at the same, or similar, depths. It is likely that a hard-water error and/or mineral carbon error is the cause of the consistently older bulk sediment dates. Mineral carbon error may be further increased due to in-wash of soils from either anthropogenically induced soil erosion or increased precipitation (Grimm et al., 2009; Oldfield, 1978). In addition, the alkalinity of water samples from Challacaba suggests it is rich in bicarbonate ions (Björck and Wohlfarth, 2001). Despite neither macrofossil being formally identified, the leaf remains were almost certainly of a non-submerged origin. Stem remains are likely to be from an emergent or submerged aquatic plant. The most modern bulk gyttia date (770–925 cal yr BP), whilst also possibly older than indicated by the bulk data, is accepted here as no other material for dating was available. It is also likely that any difference between a bulk and macrofossil date at this age would be insignificant and probably within the age uncertainty already established. The large age range of the charcoal/seed cases date, due to the small sample size, allows the date to potentially fit a spectrum of age–depth curves. The age range for the calibrated date does not overlap with our age/depth model. We hypothesize that this offset could be caused by the age of the original wood material prior to burning, at *Sacha Loma Polylepis* individuals live in excess of 60 years (Gareca, et al., 2010), and/or the retention of the charcoal in the catchment prior to incorporation into the lake sediments.





**Figure 4.2** Age–depth curve of sediment cores raised from Challacaba. Rejected  $^{14}\text{C}$  dates shown by open circles. Details of  $^{14}\text{C}$  dates given in Table 4.1.

Laboratory code	Depth (cm)	Description	$^{14}\text{C}$ Age (yr BP $\pm 1\sigma$ )	Cal. Range (cal yr BP)
SUERC-22351	91	Bulk sediment	982 $\pm$ 37	770–925
SUERC-21929	197	Leaf macrofossil	2333 $\pm$ 37	2155–2270
SUERC-22352	197	Bulk sediment	2612 $\pm$ 35	2490–2643 *
SUERC-32100	265	Micro-charcoal and seed cases	3640 $\pm$ 92	3639–4102 *
SUERC-21930	284	Stem macrofossil	3611 $\pm$ 36	3716–3933
SUERC-22355	284	Bulk sediment	4471 $\pm$ 36	4864–5071 *

**Table 4.1** Radiocarbon dates and calibrated ages for Challacaba-B core. Calibration determined using CALIB 5.1 and SHCal04 data set (McCormac et al., 2004; Stuiver and Reimer, 1993; 2010). \* = Rejected ages



#### **4.4.2) Sediments**

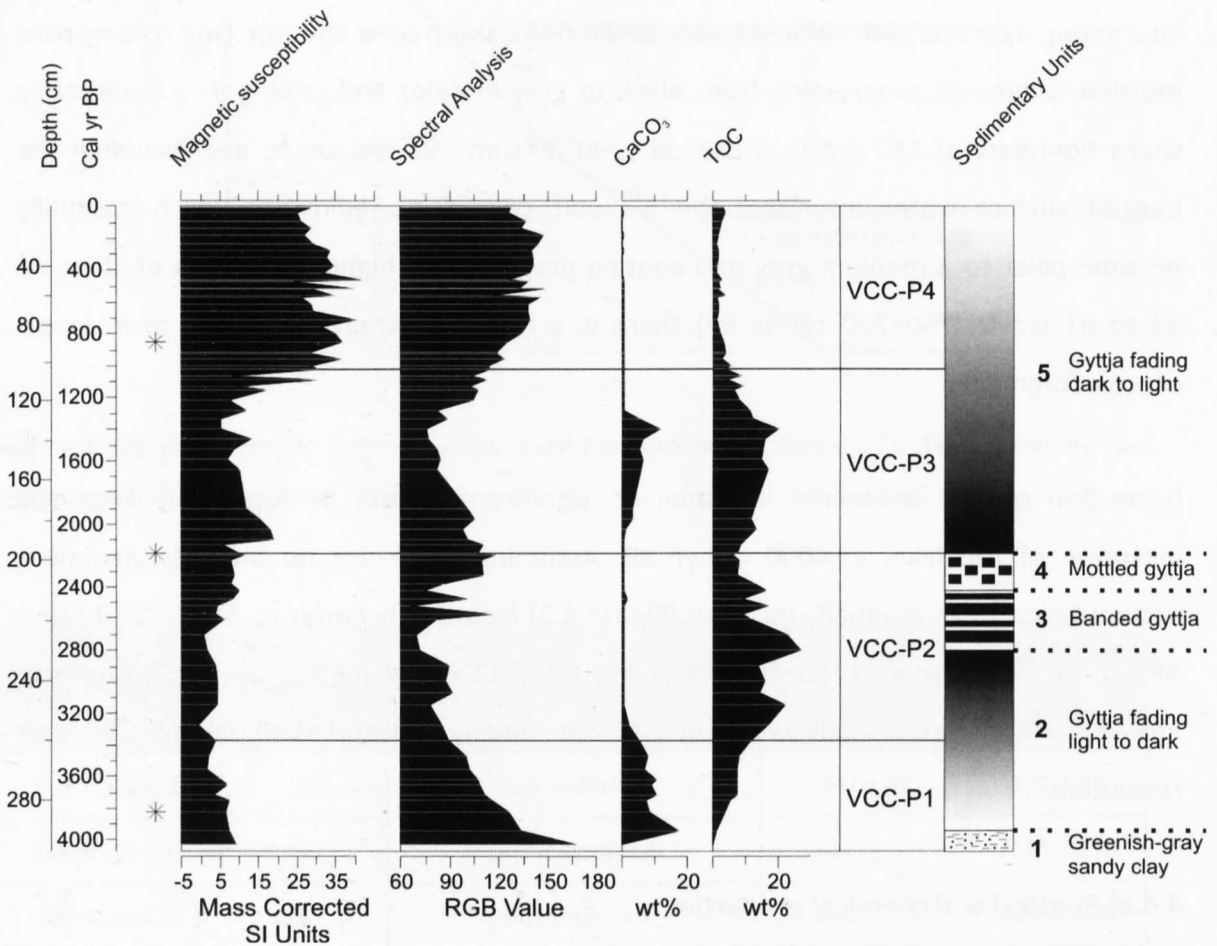
The 2.97 m core was divided into five sedimentary units (Figure 4.3). The lowest, unit 1, comprises greenish-gray sandy clay (297–290 cm, c. 4070–3940 cal yr BP). This is overlain by, unit 2, (290–230 cm, c. 3940–2800 cal yr BP), which comprises darker-colored gyttjas, with a lower sand content than unit 1 and irregular brownish bands, 1–3 cm thick, with gradational boundaries. The 3<sup>rd</sup> unit (230–210 cm, c. 2800–2420 cal yr BP) comprises alternating dark and pale colored bands and it has a sharp base and top. Unit 4 comprises mottled sediments progressing from black to gray in color and ending in a moderately sharp boundary at 197 cm (c. 2190 cal yr BP). From 197 cm, up to and including the bagged surface–water interface, the 5<sup>th</sup> unit comprises sediments which gradually become paler to a medium-gray and contain progressively higher quantities of clays. At 83 to 81 cm (c. 750–770 cal yr BP) there is a horizon comprising mainly microscopic organic fragments.

Inspection of the sediments indicates no significant breaks in deposition since the inception of the lake, c. 4000 cal yr BP. Assuming there are no hiatuses, sediment accumulation rates gradually increase (Figure 4.2) from ~0.05 cm/yr (c. 4070–2210 cal yr BP), to ~0.07 cm/yr (c. 2210–850 cal yr BP) to ~0.11 cm/yr (c. 850 cal yr BP–present). Physical and chemical analysis is sub 100 year and pollen and charcoal sub 200 year resolution.

#### **4.4.3) Physical and chemical properties**

Magnetic susceptibility (MS) and RGB color values (Figure 4.3) show similar overall trends. The RGB values shows an overall decrease from the base of the core to 225 cm (c. 2700 cal yr BP). Superimposed on this are small scale variations, with one that is particularly well marked in both the MS and RGB values between 248 and 230 cm (c. 3140–2800 cal yr BP). From 225 to 190 cm (c. 2700–2100 cal yr BP), both data sets show a higher frequency fluctuation and a generally increasing, trend. There is a sharp increase in MS values between 193 and 190 cm (c. 2140–2100 cal yr BP). After reaching their highest values in this interval, both MS and RGB show generally decreasing trends up to 135 cm (c. 1400 cal yr BP) where values are similar to those recorded at 225 cm. From 125 cm (c. 1280 cal yr BP) there is an overall increase to the highest MS values (41 SI units) seen in

the entire core and the highest RGB values (148) since the base of the core. Both MS and RGB value show high frequency and high amplitude variation in parts of this interval. There is a slight decline occurring from 22 cm (c. 200 cal yr BP) into the modern day sediment readings.



**Figure 4.3** Physical, chemical properties and lithology of Challacaba sediment cores. White lines represent sample points. <sup>14</sup>C ages shown (\*). (Wt% = weight percent. RGB = mean value of red, green and blue color intensities).

Two intervals of high  $\text{CaCO}_3$  values are evident (Figure 4.3). These span 290–248 cm (c. 3940–3140 cal yr BP) and 185–125 cm (c. 2040–1280 cal yr BP), and have maximum values of 17.2 and 11.6 wt% respectively. The remaining sediments have fairly constant low values (0.1–0.5 wt%) with the exception of a single reading of 1.4 wt% at 213 cm (c. 2480 cal yr BP). TOC values increase from the base of the core to 278 cm (c. 3710 cal yr BP) where relatively high values (>5 wt%) persist until 103 cm (c. 1000 cal yr BP). This interval of high TOC values is marked with three maxima at 248, 230 and 135 cm (22, 27 and 21 wt% respectively). From 103 cm to the core top, lower values of <5 wt%, are recorded (Figure 4.3).

#### 4.4.4) Pollen, spore and charcoal zone description

Pollen assemblage zonation was completed using the pollen taxa included in the pollen sum, *i.e.* all terrestrial pollen and excluding aquatics, spores and charcoal values. The genus *Ludwigia* (Onagraceae) was included in the pollen sum and other statistical analysis because it: i) comprises both terrestrial as well as aquatic species (Wagner, 2007), ii) is associated with lake margin habitats (Marchant et al., 2002), and iii) can be a weed in cultivated fields (Wagner, 2007). Broken stick modeling assessment concluded that four Vacas Challacaba pollen (VCC-P) zones were significant; VCC-P1, VCC-P2, VCC-P3 and VCC-P4 (Figure 4.4). In total, 88 different pollen types were identified from 38 families. 37 unknown spore/pollen types were also recorded.

##### *VCC-P1. 297–260 cm (c. 4070–3370 cal yr BP). 4 samples*

Except for the basal sample (295 cm), which contained only a few spores and damaged grains, fossil pollen concentration is high (c. 370,000–480,000 pollen grains/cm<sup>3</sup>) (Figure 4.4A). The major constituents of the pollen assemblage throughout this zone are Poaceae (20–30%), Caryophyllaceae (5–10%) and, except for one sample, Chenopodiaceae/Amaranthaceae (Cheno/Ams) (20–30%). Asteraceae, Moraceae/Urticaceae, Bromeliaceae and *Acalypha* increase towards the upper part of this zone. *Polylepis/Acaena* pollen is recorded in this zone and throughout the sedimentary succession at low levels (<7%). *Myriophyllum* (30–60%) and Cyperaceae (<2%) are the only recorded aquatics. There is also one occurrence of the green algal

genus *Pediastrum* (Figure 4.4B). Large (>180 µm) herbaceous charcoal is absent while the other fractions all show increasing trends (Figure 4.4B).

*VCC-P2. 260–197.5 cm (c. 3370–2190 cal yr BP). 8 samples*

This interval is characterized by substantially reduced fossil pollen concentrations (~8000–180,000 pollen grains/cm<sup>3</sup>) and higher percentage values of Poaceae (40–50%), Moraceae/Urticaceae and *Acalypha* (both 5–15%), although their concentration values remain constant or decrease. There are first occurrences of Piperaceae and Papaveraceae, and values of Cheno/Ams and Caryophyllaceae decreases to <9%. The aquatics *Isoëtes*, Lemnaceae and *Typha* are recorded for the first time, and both the percentage composition and concentration of *Myriophyllum* decreases. Large (>180 µm) herbaceous charcoal is recorded, and whilst rapid fluctuations are shown in the smaller wood fraction (100–180 µm), counts per cm<sup>3</sup> remain relatively high (>40) (Figure 4.4B).

*VCC-P3. 197.5–105 cm (c. 2190–1020 cal yr BP). 9 samples*

This zone has high pollen concentrations (~62,000–530,000 pollen grains/cm<sup>3</sup>) and the percentages of the majority of taxa are similar to zone VCC-P1. The most striking exception to this is the continued presence of Piperaceae, Papaveraceae and *cf. Paffia*, which were absent in zone VCC-P1. In addition *Polylepis/Acaena* is present and Juglandaceae pollen is first recorded. From c. 1470 cal yr BP a slight decline in Caryophyllaceae and an increase in *Acalypha* are shown. *Myriophyllum* and Cyperaceae again dominate the aquatic assemblage and from c. 1210 cal yr BP a maxima (80%) in *Pediastrum* occurs. This is accompanied by the first significant amount of spores of the dung fungus *Sporormiella* (Figure 4.4B). Charcoal particles levels are similar to the two previous zones but all size fractions show a well defined and large magnitude decrease trend by c. 1340 cal yr BP.

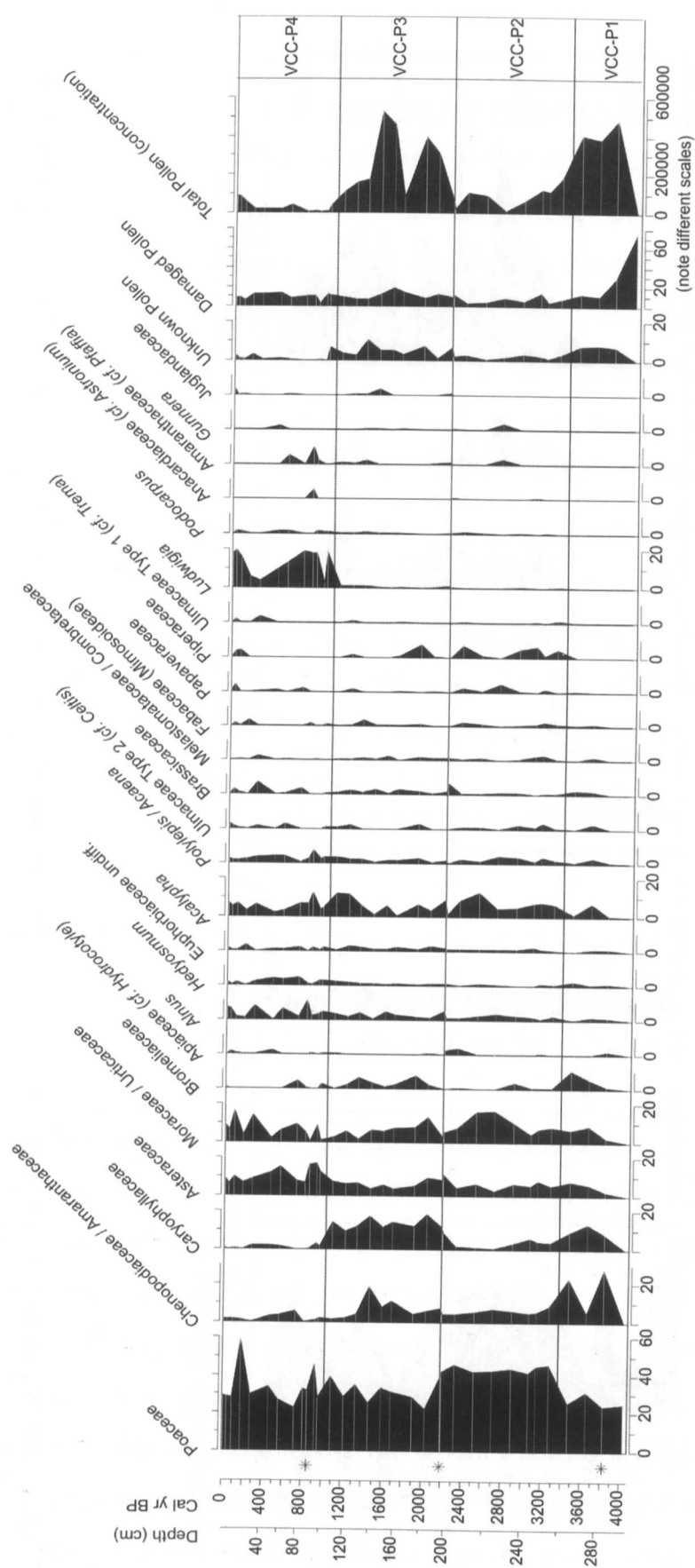
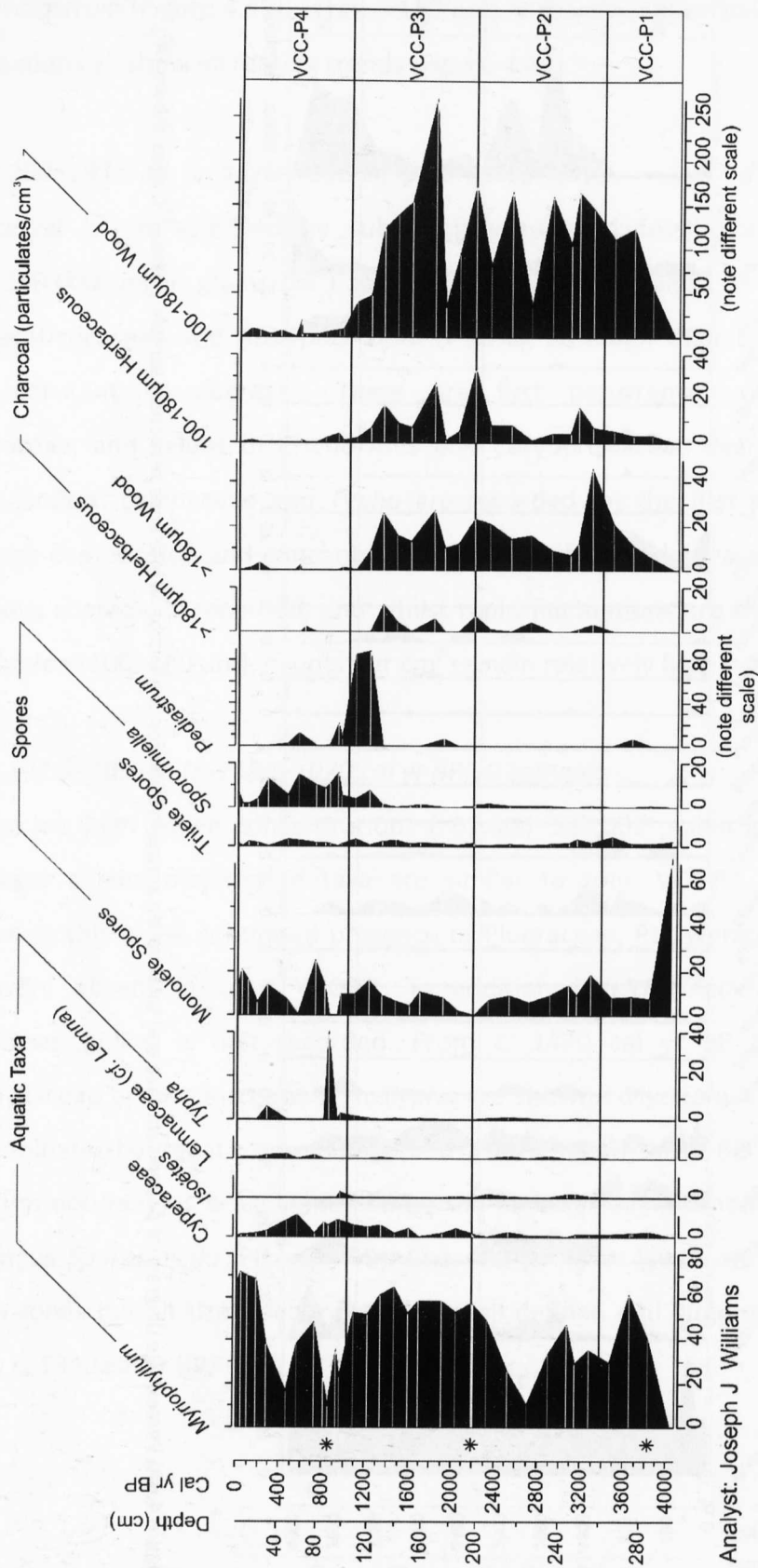


Figure 4.4A) Percentage diagram of pollen sum taxa and total pollen concentration for Challacabca. White lines represent sample points. <sup>14</sup>C ages shown (\*).



**Figure 4.4B)** Percentage diagram of aquatic taxa, spores and algae for Challacaba. Carbon particulates shown in counts per cm<sup>3</sup>. White lines represent sample points. <sup>14</sup>C ages shown (\*).

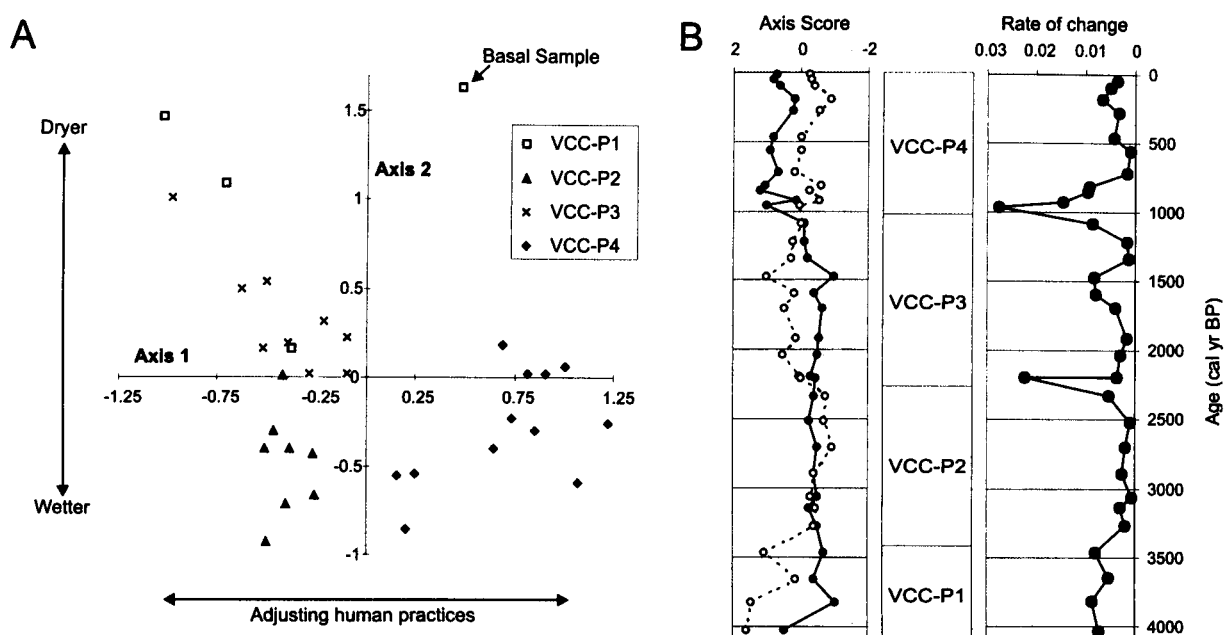


*VCC-P4. 105–0 cm (c. 1020–0 cal yr BP). 12 samples*

Characterized by the appearance and significant percentage of the wetland associated genus *Ludwigia*, this zone represents the period of lowest fossil pollen concentration (~4000–90,000 pollen grains/cm<sup>3</sup>). Caryophyllaceae percentages are substantially reduced (<3%), and *Alnus*, *Hedysmum*, cf. *Pfaffia*, Brassicaceae and Asteraceae reach previously unattained high levels. Whilst Chen/Ams percentages are reduced a slight increase (3–6%) is recorded between 77 and 50 cm. *Polylepis/Acaena* reaches its highest percentage in this zone, up to 3–6%, but show large fluctuations. As in zone VCC-P3, *Myriophyllum* percentage is generally low until 20 cm (c. 190 cal yr BP). Lemnaceae (0–2%) and *Typha* (0–40%) abundances fluctuate throughout VCC-P4, while Cyperaceae maintains the high levels from the previous zone (VCC-P3) before showing a decreasing trend from c. 560 cal yr BP till the modern day. *Sporormiella* is present throughout this zone but does show a decreasing trend from c. 190 cal yr BP. *Pediastrum* is present at mid to low values in 5 sample depths. A large scale reduction of all charcoal fractions is evidenced throughout this zone (Figure 4.4B).

*Ordination*

NMDS ordination was run to explore trends within the variability of the pollen sum data. NMDS was preferred as it makes no assumption as to the distribution of the variables (McCune and Mefford, 2006). The ordination was run using the pollen sum taxa with rare types (<3% abundance) removed. A 3-dimensional solution was then chosen with distance relationships established using Sorensen's index (Bray–Curtis). Final stress levels stabilized at 9.06% after 109 iterations. After examination of the output data, axis 1 and 2 scores are plotted against time (Figure 4.5B). The biggest changes occur during the transitions from VCC-P2 to P1 and VCC-P4 to P3. The ordination plot (Figure 4.5A) demonstrates how samples from different zones plot in distinctly different spaces. The most spatially separate sample relates to the very base of the core (295 cm) which has high values in both axis one and two. The rate of change (Figure 4.5B) is calculated as the Euclidean distance between two adjacent samples, divided by the time between them (see Urrego et al., 2009). While this ordination can provide us with a rudimentary rate of change (RoC), a more robust chronology would be required to refine this sufficiently and make it comparable to other studies.



**Figure 4.5** Results of NMDS of pollen sum taxa for Lake Challacaba. **A)** Ordination plot of sample scores for Axis 1 and 2. Point symbols refer to relevant attributed zone. **B)** Axis 1 (solid line) and Axis 2 (dashed line) scores (left graph), and rate of change (right graph) both plotted against time.

## 4.5) Environmental reconstruction and discussion

### 4.5.1) Late Holocene climatic changes: moisture balance fluctuations

The Challacaba lake formed at c. 4070 cal yr BP as shown by the deposition of lake sediments on top of what is interpreted to have been windblown deposits. The very basal sample (295 cm) attests to this period of lake formation as pollen grain concentration is low and preservation poor. Spores, which are more robust to the affects of oxidation, dominate (Figure 4.4B). The basal sample at 295 cm, plots in a unique space on the NMDS ordination (Figure 4.5A), indicating its general dissimilarity to all other samples.

The relatively higher quantity of sand present in the sediment from 297 to 290 cm (c. 4070–3940 cal yr BP) (Figure 4.3), supports the pollen and spore data and suggests a shallow, ephemeral lake. The transition from sandy silt to gyttia deposits, sometime before 3820 cal yr BP, indicates the point at which the basin center became more or less continually inundated. The presence of a permanent water body resulted in improved microfossil preservation and deposition of a local to regional scale pollen assemblage. The multi-proxy analysis of the sediment cores, indicates two periods of reduced moisture

availability (pollen zones VCC-P1 and VCC-P3) and two adjacent wetter episodes (VCC-P2 and VCC-P4).

After the (c. 250 yr) period of lake stabilization, high abundances of drought-tolerant vegetation (Caryophyllaceae, Chenop/Ams and Bromeliaceae) (VCC-P1; Figure 4.4A), are evident.  $\text{CaCO}_3$  has been shown in other Andean records to be an indicator of dry events and lowered lake levels (Baker et al., 2001; Hillyer et al., 2009). High  $\text{CaCO}_3$  values (up to 17.2 wt%) (Figure 4.3) at Challacaba during VCC-P1 are therefore interpreted here to indicate that the lake was not overflowing and that water level was lower than today. Although zone VCC-P1 is considered a period of reduced moisture availability compared to other periods of the Challacaba record, the zone does represents a reduction in drought events which dominated the mid-Holocene dry phase between c. 8000 and 5000 years ago.

The VCC-P1 period reconstructed from Challacaba supports the water level history reported from Lake Titicaca (~370 km north-east). Abbott et al. (1997), indicate a regional climate influence and suggest lake levels were at their lowest prior to 3500 cal yr BP, and that the mid-Holocene dry phase ended abruptly between 3500 and 3350 cal yr BP. Challacaba seems to have undergone a more gradual transition out of the mid-Holocene dry phase, but it is considered likely that Challacaba lake formation is linked to this wide, regionally recognized, moisture signal. In the Eastern Andes, other sediment records also attest to the presence of the mid-Holocene dry phase, either by lowered lake levels (*e.g.* Lake Consuelo; Urrego et al., 2010) or post event lake formation (*e.g.* Marcacocha; Chepstow-Lusty et al., 1998).

The increase in regional moisture, which led to the inundation of the Challacaba lake basin could have been caused by a resumption of more “normal” (less declined) ENSO activity following the “weak” El Niño regime that it has been suggested dominated during the mid-Holocene period, 8–5.6 ka (Rein et al., 2005). The timing of formation of Challacaba does not concur with that of nearby Juntutuyo (Abbott et al., 2003), which shows lake development some c. 1500 years later. This may be a result of Challacaba being fed, in part, from the surrounding hills to the east and/or that the Juntutuyo core

record of  $\text{CaCO}_3$  was not taken from the deepest part of the lake (Abbott, M., personal communication, 2010). There is no evidence to suggest that a local tectonic change created a depression in which Challacaba formed.

The initial phase at Challacaba (VCC-P1) persisted until a change some time between 3460 and 3270 cal yr BP where arid and salt tolerant vegetation, particularly Cheno/Ams, begin to decline,  $\text{CaCO}_3$  wt% decreases and TOC begins to increase. The ordination of samples from the first wetter phase, VCC-P2, shows a distinct clustering with negative scores in both axis 1 and 2 (Figure 4.5A). A marked decrease in fossil pollen concentration throughout VCC-P2 is here interpreted to show an increased areal extent and deepening of the lake and thus a dilution of the pollen input. This conclusion is supported by the decreased percentage of *Myriophyllum*, a genus which has been observed to predominate in shallow waters, 0.4–4 m (Ybert, 1992), as it becomes further removed from the core location at the lake depth maxima. The shift towards a wetter interval again correlates well to an increase in ENSO variability recorded at Laguna Pallcacocha in southern Ecuador sometime from 3500 to 3400 cal yr BP (Moy et al., 2002).

From c. 2190 to 1020 cal yr BP (VCC-P3) a shift in the NMDS ordination (Figure 4.5A) highlights a change in the pollen data which, in our interpretation, suggests a return to conditions of reduced moisture; this is particularly well demonstrated by an increase in Caryophyllaceae (10–19%), which favors dry conditions. In addition Cheno/Ams and Bromeliaceae percentages increase as does the total pollen concentration (Figure 4.4A). While the vegetation does share many similarities with that immediately after lake formation (VCC-P1), important differences exist, the most noticeable being the continued presence of Piperaceae and the gradual continued increase of Cyperaceae. This second interval of drier conditions, is supported further by significantly higher  $\text{CaCO}_3$  concentrations between c. 1970 and 1340 cal yr BP, suggesting a lowered lake level.

From c. 1020 cal yr BP (VCC-P4) a reduction in the abundance of arid and salt tolerant vegetation, together with the much lower concentrations of  $\text{CaCO}_3$ , we interpret to indicate a return to conditions that, on average, were locally wetter than the previous period (VCC-P3). As in the previously recorded wet period, VCC-P2, *Myriophyllum*

percentage is generally reduced. The very low pollen concentration values are, at least in part, a result of the dilution effect of a larger lake, but it is also possible that this reflects a less productive landscape (*i.e.* less vegetation cover). We recognize however that short phases of increased aridity, particularly regional scale ones, may have occurred within this period that are not represented in the limnological record either due to their duration or a buffering effect of the locality. Nonetheless, the apparent shift to on average wetter conditions at Challacaba could be related to a more widespread Andean trend of ENSO events as evidenced in the Laguna Pallcacocha record. At Pallcacocha a frequency maximum has been identified at *c.* 1200 cal yr BP and a general increased number of ENSO events between *c.* 900 and 300 cal yr BP, albeit punctuated with shorter term reductions and a steadily declining frequency trend. (Moy et al., 2002).

Intriguingly, the pollen spectra recovered from VCC-P4 is markedly different to that of the previous wet interval (VCC-P2). The NMDS ordination (Figure 4.5A), whilst supporting the general conclusion that samples aging from *c.* 1020 to 0 cal yr BP display a wetter environment signal (more negative values on axis 2), also highlights that from 1030 cal yr BP, the pollen assemblage is distinctive from that of VCC-P2 (less negative values on axis 1). In addition, the maxima in the RoC score that centered around the VCC-P2 to VCC-P1 boundary (*c.* 1020 cal yr BP) (Figure 4.5B) indicates a major vegetation change in the Challacaba record that we associate here with an adjustment in human activity.

While the Challacaba record supports the conclusion that a period of increased moisture availability existed during the zone VCC-P4, adjusting human impact on the local landscape undoubtedly complicates the signal of moisture fluctuation. With this mind, we interpret the period after *c.* 1020 cal yr BP, to primarily represent a time of changing, possibly increasing, human impact levels. The site of Marcacocha also points to increasing human activity around this time as indicated by both archaeological and sedimentary records (Chepstow-Lusty et al., 2009). However, the Marcacocha record has been interpreted to indicate a temperature increase from around *c.* 900 cal yr BP which led to warm and relatively stable conditions, but crucially, without any associated increase in precipitation (Chepstow-Lusty et al., 2009). While we are unable to speculate if warmer conditions might also have begun at Challacaba around this time, due to the lack of an

independent temperature proxy, we interpret the combined data sets here to indicate a general increase in the moisture availability, which could be linked to either changes in temperature, precipitation or both.

#### 4.5.2) Changing human activity

The high level of charcoal from the start of the Challacaba record ( $> 50$  particulates /  $\text{cm}^3$ ) probably indicates that people have utilized this area continually from at least c. 4000 cal yr BP (Figure 4.4B). The high abundance of large woody charcoal fragments and low levels of woodland pollen taxa between c. 4030 and 1090 cal yr BP suggests that people were possibly transporting fuel wood collected elsewhere to burn close to the lake. The earliest indicator of trading and pastoralism is recorded by a marked rise in fungal dung spores, and tentatively algal remains c. 1280 cal yr BP (Figure 4.4B). As neither of these biological groups were included within the pollen sum, they have no influence upon the statistical zonation or the NDMS ordination.

The first significant occurrence ( $>2\%$ ) of *Sporormiella* fungal spores in the core occurs at c. 1340–1210 cal yr BP (Figure 4.4B). *Sporormiella* is a coprophilous ascomycete fungus common on the dung of herbivores (Ahmed and Cain, 1972). Recent work on modern lakes acknowledged *Sporormiella* as a useful proxy to indicate herbivore presence, but highlighted a strong positive relationship between proximity to shoreline and *Sporormiella* abundance (Raper and Bush, 2009). However, in the case of Challacaba, the *Sporormiella* increase coincides with a transition from drier to wetter conditions as attested to by both the terrestrial palynological and the geochemical data indicating that the lake shoreline became further away from the coring site. We can therefore be confident in the assessment that herbivore presence around Challacaba substantially increased between c. 1340 and 1210 cal yr BP. The increase in *Sporormiella* is concurrent with the oribatid mite record from Marcacocha, which shows a progressive increase in livestock number, from c. 1200 cal yr BP (Chepstow-Lusty et al., 2007).

Challacaba is the freshest lake in the Vacas Lake District and is located close to a narrowing of the valley which constrains the historic road running east to Inkallajta (Figure 4.1A). It therefore seems likely that any pre-Columbian increase in dung



deposition surrounding the lake would have been due to an increase in domesticated camelids (alpaca and llama herds) being watered at the lake whilst being driven along the road. The tendency of camelids to defecate in restricted communal piles, often close to a water source (Sillar, 2000) adds weight to this interpretation. While the primary rise in camelid numbers, inferred from the increased abundance of *Sporormiella*, coincides with archaeological evidence indicating Tiwanaku cultivation expansion between 1200 and 1000 years ago, it is possible that a second increase in *Sporormiella* seen in the Challacaba record (c. 920 cal yr BP) is related to Tiwanaku fragmentation. The abandonment of urban centres around Lake Titicaca is evidenced by a silence in monument construction between c. 800 and 500 years ago, which may represent a dispersal of people into new, more rural, lands (Albarracin-Jordan, 1992; Binford et al., 1997; Kolata, 1993).

Two multi-centennial dry events (c. 1410–1190 and 850–550 years ago) that have been associated with the collapse of Tiwanaku (Binford et al., 1997) do not appear to have had as much a dramatic impact on the terrestrial vegetation or the human impact levels around Challacaba (Figure 4.4A). Given the current chronology available it is difficult to tie the Challacaba record to these rapid fluctuations; however the Challacaba record does hint at responses that are roughly concurrent with this dry–wet–dry oscillation noted around Lake Titicaca: i) the decrease in  $\text{CaCO}_3$  in Challacaba at c. 1270 cal yr BP coincides with the end of the first of these dry episodes (Figure 4.3), ii) the peak in *Pediastrum* (c. 1210–920 cal yr BP) straddles the intervening wet period (Figure 4.4B), iii) the peak in *Typha* (c. 850 cal yr BP) coincides with the onset of the second dry period (Figure 4.4B), and iv) drought tolerant Cheno/Ams values are slightly elevated (c. 720–470 cal yr BP) through the second dry episode (Figure 4.4A). The absence of elevated  $\text{CaCO}_3$  during the second dry phase may be due to camelid dung acidifying the lake. The persistence of high *Sporormiella* values through these postulated short-term lake level fluctuations supports the interpretation that the rise in *Sporormiella* is due to a higher numbers of camelids visiting the lake.

Simultaneous with the initial herding increase (c. 1270 cal yr BP) a maximum in the algal genus *Pediastrum* is also detected. This algal peak is interpreted to reflect an adjustment in lake nutrient status. Whilst other studies have interpreted lake eutrophication to be a

result of increased nutrient in-wash after deforestation (Paduano et al., 2003; Woodward and Shulmeister, 2005), we here suggest that a direct input of nutrients from a local increase of animal activity is responsible. The *Pediastrum* maxima of 88% are simultaneous with the arrival of substantial quantities of camelids for the first time, as indicated by the abundance of *Sporormiella* spores. Two later increases in *Sporormiella* (c. 920 and 560 cal yr BP) also correlate to *Pediastrum* blooms, albeit ones of lower magnitude.

The large increase in *Ludwigia* marks the transition from zone VCC-P3 to VCC-P4. *Ludwigia*, as discussed previously, is a genus generally associated with wetland habitats (Marchant et al., 2002). The increased abundance of *Ludwigia* is contemporaneous with the reduction in arid and salt tolerant taxa and we interpret the pollen record from c. 1020 cal yr BP to represent vegetation composition typical of an increased marshy habitat, created as the lake level rose and water inundated the flat expanse of the north and east shores.

The sudden increase of *Ludwigia* at this time and lack of a similar abundance during the early wetter phase (VCC-P2) may be linked to human influence. The arrival of increased camelid numbers and thus nutrient input, together with increased grazing on existing moist vegetation (aquatics), may have led to the creation of a niche space suitable for *Ludwigia* to exploit. *Ludwigia* is an invasive species and it is plausible that its arrival in the Challacaba region is related to the transport of *Ludwigia* seeds by camelids from wetlands they have previously visited. The sporadic increase in *Typha*, that is seen through zone VCC-P4, could also indicate a response to changing nutrient status through this time (Marchant et al., 2002).

#### **4.5.3) Fire history**

There appears to be no connection between the fire history and the wider vegetation signal at Challacaba and we attribute the majority of carbon particulates throughout the last 4000 cal yr BP to be from local anthropogenic sources (fuelwood for cooking, heating and possibly some clearance burning). The main shift occurs from c. 1340 cal yr BP when all size fractions show a dramatic decreasing trend and by c. 1020 cal yr BP, the start of

VCC-P4, particulate counts are consistently under 20 per cm<sup>3</sup> (Figure 4.4B). A similar scale decrease was found in the Titicaca record (Lago Grande), as particulates declined and ultimately disappear after 2 ka (Paduano et al., 2003). Paduano et al. associated the decline in charcoal at Titicaca with a reduced availability of fuelwood, as supported by a concomitant woodland pollen decrease. At Challacaba there is no palynological evidence for decreased woodland cover instead the decline in charcoal abundance is coincident with the rise in camelid dung fungus.

In many rural Andean regions today dried cattle dung acts as a main energy source and in Bolivia it accounts for 19% of total biofuel (Winterhalder et al., 1974; World Bank, 1994; Yevich and Logan, 2003). Since wood has been a scarce resource in these environments for a considerable time, including Tiwanaku times, camelid dung has long provided an alternative fuel for fires (Janusek, 2008). While traditionally the importance of dung burning may have its origins in pottery firing, its long term historical use suggests that during times of increase camelid numbers, dung supply would have been greatly increased and so would its utilization in a much wider context (Sillar, 2000). It therefore seems plausible that between c. 1340 and 1020 cal yr BP the people travelling through the Vacas region switched from collecting, or possibly travelling with or trading fuelwood, to the utilization of dried dung.

#### **4.5.4) The *Polylepis* woodland / grassland matrix**

Through the duration of Challacaba record, except for two samples (basal and 2190 cal yr BP), *Polylepis/Acaena* pollen has low abundances (0.2–6.6%). It is assumed that the pollen recorded here is predominantly from the tree genus *Polylepis* rather than *Acaena*; the latter is a herb genus associated closely to moist valleys, typically within cloud forests (Chepstow-Lusty et al., 2005; Weng et al., 2006).

As discussed in Section 1.1.2, some modern ecological data suggest that today the high Andean *Polylepis* woodland only covers around 10% of its potential distribution (Fjeldså and Kessler, 1996). However, the fossil pollen record from Challacaba shows no evidence for a reduction in *Polylepis* woodland cover around Vacas during the last 4000 yr. The continually low abundance at Challacaba is contrary to the decline in *Polylepis* pollen at c.

3100 cal yr BP evident from Lake Titicaca (Paduano et al., 2003) but parallels the c. 4000 yr record from Marcacocha (Peru) (Chepstow-Lusty et al., 1998).

The regionally variable pattern of the past *Polylepis* woodland extent emphasizes uncertainty in the assumption that the natural state of the Andes is a continuous belt of a permanent *Polylepis* woodland (*sensu* Ellenberg, 1958), and supports the case for persistent regional variability defined by microclimate conditions (Gosling et al., 2009). Given the long history of human occupation of the Andes it is possible that woodland clearance was completed prior to the formation of the Challacaba record (pre c. 4000 cal yr BP), or that the *Polylepis* forests never recovered after the mid-Holocene dry period, as around this time major human impact (agriculture) in the Andes began. However, the vegetation reconstruction presented here shows only minor fluctuation in the grass to *Polylepis* woodland matrix through the period of major regional pre-Columbian cultural expansion and contraction.

The conclusion of late Holocene *Polylepis* woodland stability is supported by Lake Pacucha pollen record in the central Peruvian Andes, which represents a site for continuous human occupation for at least the last 4000 years (Valencia et al., 2010). At Pacucha there is no evidence for *Polylepis* woodland reduction in response to human activity. The *Polylepis* woodland was most abundant during deglaciation (c. 16000–14000 cal yr BP), which parallels new findings from the pollen record of Laguna Khomer Kocha Upper (17°16' S, 65°43' W; 4153m elevation), situated 40 km north-west of Challacaba (Chapter 5).

#### **4.6) Conclusions**

The complete paleolimnological history of Lake Challacaba reveals that vegetation change in the Cochabamba Basin, Bolivia, has been driven by both human and climatic factors during the last 4000 years. Two distinct drier than modern stages; before c. 3370 and 2190–1020 cal yr BP are recorded. The older dry event can be linked to the latter stages of lower regional moisture availability caused by the “weak” El Niño system that dominated during the mid-Holocene (Rein et al., 2005). The second drier interval, whilst

likely to be again related to a regional ENSO signal, is less clearly correlated with other records. Between the Challacaba dry phases there was an interval of increased moisture availability (c. 3370–2190 cal yr BP).

Although the pollen data from Challacaba may suggest a shift to generally wetter conditions from c. 1020 cal yr BP, it is likely that shorter term reductions in the moisture balance occurred throughout. Ultimately however, there is strong evidence to show that a change in human activity at some point between c. 1340 and 1210 cal yr BP was a major factor in shaping the modern regional landscape. The pollen assemblage from the last 1000 years is very different to that from any other time during the preceding 3000 years. The charcoal record indicates that the local ecosystem has been under anthropogenic influence for the duration of the time spanned by the Challacaba core (c. 4000 yrs). As such we are unable to obtain a baseline record for what is the natural state of the ecosystem without human influence, but, it is evident that overall the *Polylepis* woodland maintained a relatively stable presence and abundance even during the height of human pressure.

This research supports the interpretation that the Vacas Lake District was an important point on the ancient roadway network during pre-Columbian times. Further work is required to clarify the extent to which the observed changes in human activity are a product of unconnected wider social changes or a smaller scale local impacts. In particular, refining the chronology of the sequence will help to better constrain the timings of significant environmental changes observed within the record and this will be critical if they are to be linked to any known cultural events.

#### **4.7) Acknowledgements**

This research was funded by a NERC Open CASE studentship with the Natural History Museum, London (NE/F008082/1), NERC radiocarbon facility support (1287.0408 and 1463.0410) and a National Geographic Committee for Research and Exploration grant (8105–06). Finally, we are grateful for the comments of Alex Chepstow-Lusty and Henry Hooghiemstra whose vigorous evaluations helped to substantially improve the strength of this manuscript.

## Chapter 5)

### ***The sensitivity of eastern Andean vegetation to climate and fire***

In this chapter, all fossil pollen, spore, charcoal, geochemical and geophysical data from the Laguna Khomer Kotcha Upper study site are presented and discussed. This chapter has been submitted for publication separately:

**Williams, J.J.**, Gosling, W.D., Brooks, S.J., Coe, A.L. and Xu, S. The sensitivity of eastern Andean vegetation to climate and fire.

*Palaeogeography, Palaeoclimatology, Palaeoecology* (Submitted April 20, 2011).

---

#### **5.1) Abstract**

A c. 18 ka cal BP long sediment record from Laguna Khomer Kocha Upper (4153 m asl), Bolivia, shows that fire regime, governed by climatic variation, has long been a transformative agent in the eastern Andes. Before c. 14.5 ka cal BP, warming and relatively moist conditions free from fire, facilitated the expansion of high Andean *Polylepis* woodland. Fire onset at c. 14.5 ka cal BP, quickly transformed the local vegetation and the woodlands became restricted to areas protected from fire. A major increase in burning at c. 10.1–6.4 ka cal BP removed *Polylepis* woodland locally and this is correlated with a region-wide Holocene dry event (HDE) which caused falling lake levels and allowed fire intensification. A decline in burning at c. 6.4 ka cal BP and an increase in marsh-woodland (*Alnus*) marks the termination of the HDE and the return to wetter conditions. As well as recording the environmental history of local vegetation dynamics, long-distance pollen transport provides evidence of changes in the montane forests, highlighting their sensitivity to climate and burning regimes. Simultaneous adjustments in both Andean and lowland taxa suggests that vegetation dynamics in the two environments are linked to a common climatic driver. There is no evidence to indicate that human activity had any impact on the local landscape.

## 5.2) Introduction

Worldwide, mountainous regions provide early warning for changes in environmental processes and climate change (Ørbæk et al., 2004; Tiberti et al., 2010). In the Tropical Andes, one of the richest and most biologically diverse regions on Earth (Myers et al., 2000), future climate changes are considered a serious threat to biodiversity (Malcolm et al., 2006). High biodiversity levels are partly attributable to the complex topography and large elevational range (2500-4500 metres above sea level [m asl]) which supports many microclimates. The extreme altitudinal variation means that continuous montane forests can be found within just a few tens of kilometres of grassland and bare rocky peaks (Bush et al., 2007; Young et al., 2002). The narrow vertical species ranges mean that even small variations in temperature or precipitation can result in considerable changes in species distribution. This sensitivity allows the evaluation and monitoring of change, not only of modern floras (e.g. Feeley et al., 2011; Sarmiento et al., 2003) but crucially, via the use of palaeolimnological investigation, of long-term shifts in response to climatic changes in the past (e.g. Bush et al., 2004; Cárdenas et al., 2011).

In the Andes, the climate of the Last Glacial Maximum (LGM;  $21 \pm 2$  thousand years before present [ka cal BP]; Mix et al., 2001) was 7–8°C cooler than today (on the Altiplano) and moisture availability varied regionally (Baker et al., 2003; Cook, 2009; Sylvestre, 2009). Moisture balance fluctuated throughout the deglaciation period and the Holocene (11.7 ka cal BP to present) and there was small-scale variation in temperature (Bush et al., 2005). Although the timings, impacts and mechanisms driving environmental change in the Andes during this period are still debated, the response of the environment to key global events have been determined and include warming during the Bølling-Allerød chronozone (c. 15–14.0 ka cal BP), a cold event during the Younger Dryas chronozone (c. 12.9–11.6 ka cal BP) and a mid-Holocene dry event (MHDE) (c. 8–5 ka cal BP; Rasmussen et al., 2006; Sandweiss et al., 1996; Thompson et al., 1998; Urrego et al., 2009; Zech et al., 2010). Adjustments in climate systems such as the El Niño-Southern Oscillation (ENSO; e.g. Moy et al., 2002), the South American Summer Monsoon (SASM; e.g. Vuille and Werner, 2005), and the Intertropical Convergence Zone (ITCZ; e.g. Leduc et al., 2009) have also been highlighted as important drivers of climatic signatures observed within palaeorecords.



As more records become available, it is apparent that the impact, scale and nature of climate events have been spatially non-uniform across the Tropical Andes (Bush and Gosling, 2011). Local factors, including human occupation, often disguise regional patterns. In addition, the distribution of study locations is unevenly spread and many regions, which are climatically sensitive today, remain unexplored palaeoclimatologically and are unrepresented in regional-scale studies.

The biodiversity of the Tropical Andes is also vulnerable to increasing human occupation (Cincotta et al., 2000). Although human populations have existed in South America since the late Pleistocene (pre 11.7 ka cal BP) (Coltorti et al., 2010; Lynch, 1990; Roosevelt et al., 1996), the extent of human environmental impact is inconclusive and variable (Bush et al., 2008). The early use of fire by humans in the Andes (Ellenberg, 1979) can potentially be traced in palaeoenvironmental record through the examination of fossil charcoal (Whitlock and Larsen, 2001). However, evidence that fire has been a natural component of central Andean ecosystems long before the arrival of humans (Gosling et al., 2009; Hanselman et al., 2011; Paduano et al., 2003), adds complexity in distinguishing a human or natural signal. In addition, the subsequent development of human cultures (e.g. Wari, Tiwanku, Inca) led to changes in resource-use and land-use, and a variation in the human impact on the landscape through time (Chapter 4; Williams et al., 2011).

The period since the LGM is critical for understanding human-climate-ecosystem interactions in the central Tropical Andes because it is: i) when the last major global climatic transition occurred (full glacial to interglacial conditions), and ii) when humans spread throughout South America. As a result, the deglaciation and early Holocene period is the most recent time in which central Tropical Andean ecosystems were not substantially influenced by human practices, but were exposed to natural stress. Understanding long-term ecological shifts in response to past environmental change is fundamental to the development of effective conservation and management policies (Godwin, 1956; Willis and Birks, 2006).

In this study, we present the findings of a new palaeolimnological record from the moist mountain ranges northeast of the Cochabamba Basin, Bolivia (Figure 5.1A). These eastern slopes, where moist air from the Amazon collides with the Andean mountain chain, is one of the most biologically rich areas on Earth (Killeen et al., 2007). However, it is on these flanks above 3500 m asl that climatic models predict some of the greatest environmental changes will occur (4–5°C rise by 2100; Urrutia and Vuille, 2009). The sediment record of Laguna Khomer Kocha Upper, situated 4153 m asl, is ideally placed to provide insights into past environmental change in the complex and sensitive landscapes linking Western Amazonia to the Andean mountain ranges. Multi-proxy analysis (geochemical and physical properties, fossil pollen, spores and charcoal) of lake sediments, at sub-millennial resolution, has allowed the detailed reconstruction of the environment (vegetation, precipitation, temperature and fire) of the eastern Bolivian Andes for the first time.

### **5.3) Study location**

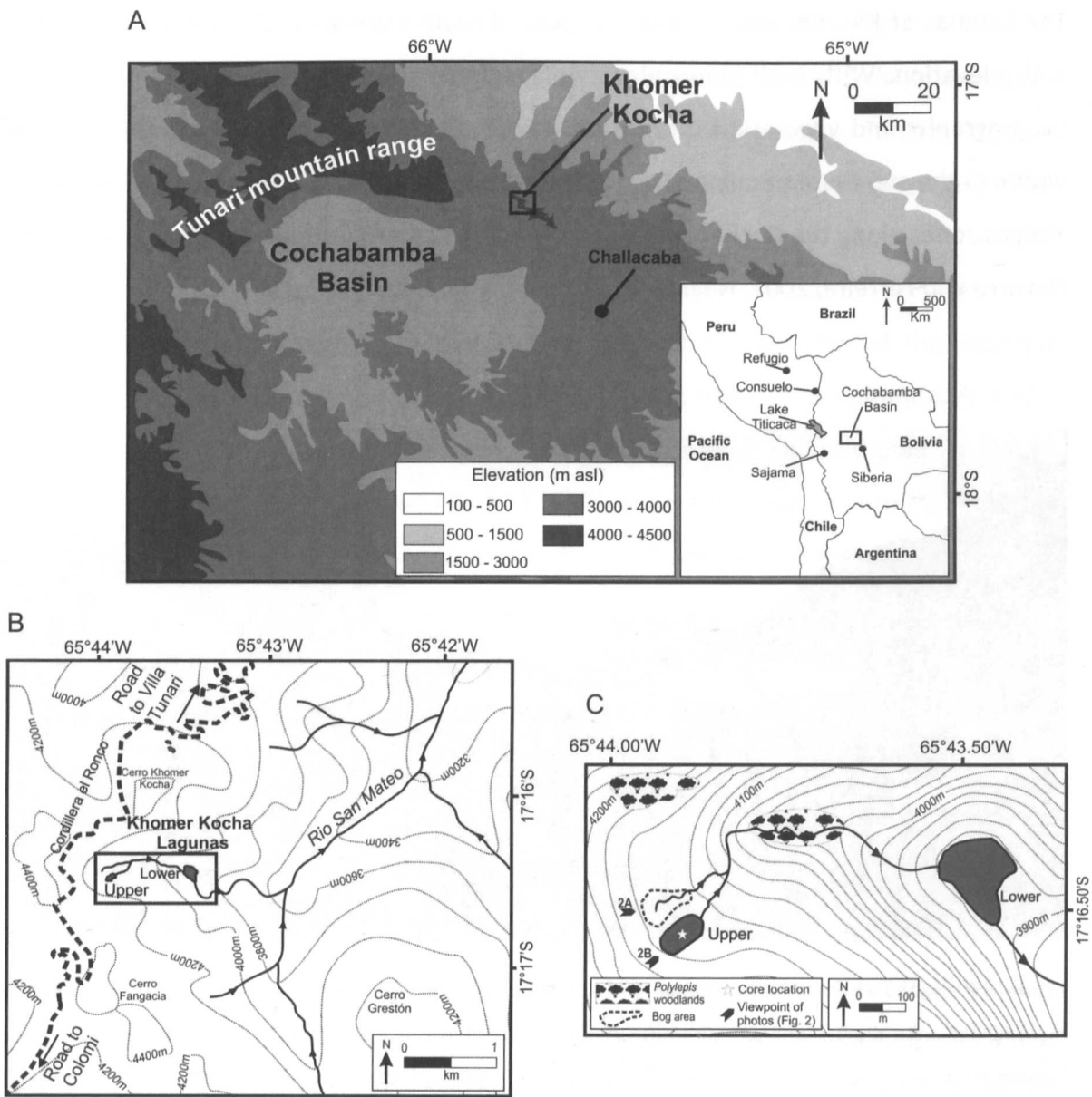
Laguna Khomer Kocha Upper is a small, ~0.007 km<sup>2</sup>, glacially formed lake with a maximum depth in June 2007 of 3.6 m (17°16.514' S, 65°43.945' W; 4153 m asl). Previously unnamed, we refer to the lake as Laguna Khomer Kocha Upper (LKKU), as it is situated <800 m to the west and ~250 m above Laguna Khomer Kocha (~3900 m asl). On the slopes of the Cordillera el Ronco, the lake overlooks the tributaries of the Rio San Mateo, a valley which descends more than 2000 m elevation in less than 10 km (Figure 5.1B). The site is accessed by a track leading from Aguirre to Villa Tunari, which passes along the western limits of Carrasco National Park.

The southwest and southeast sides of LKKU consist of steep, but seemingly stable, slopes dominated by tussock-forming Andean grasses (Figure 5.2A and B). The northwest side is created by a glacial deposit, ~2 m in height, running the length of the lake (~110 m). This moraine separates the lake from an area of flat, waterlogged ground, which probably represents an in-filled lake of similar size to LKKU (Figure 5.1C and 5.2A). The lake is fed by runoff from the surrounding slopes. While LKKU was not overflowing during our visit, an outflow channel to the northeast cuts through a small moraine before descending into a steep, wooded (*Polylepis* sp.) gully towards Laguna Khomer Kocha (Figure 5.2B). The following lake-water variables were measured in June 2007: turbidity (secci depth) 3.2 m;

conductivity 28  $\mu\text{S}$  (microSiemens) per  $\text{cm}^{-1}$ ; pH 7.38. All values are means of three readings and no long-term data are available.

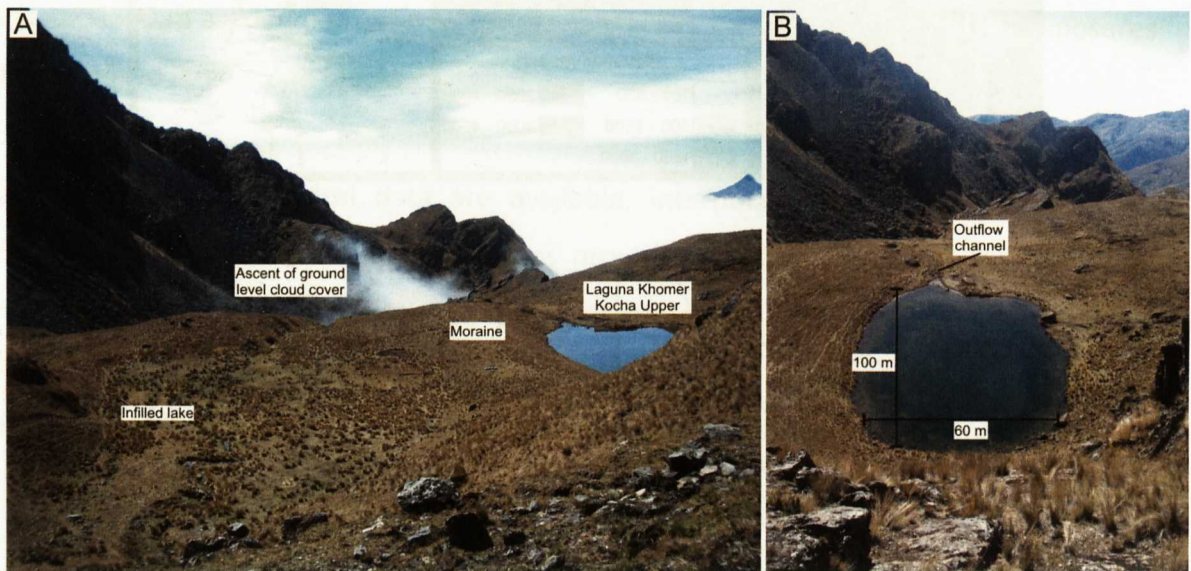
The local geology is not known in detail. However, regionally the bedrock consists mainly of sandstones, lutites and quarzitic rocks of Ordovician age (488.3–443.7 Ma), with areas of granite intrusions (Cassard, 1999; Kessler, 2002b). Calcareous rocks have been found between 2000–2200 m asl (Kessler, 2002b). Peaks in the Cordillera el Ronco reach elevations above 4500 m asl but no permanent snow-line was observed in June 2007. Above ~4300 m asl, large proportions of the landscape are dominated by rock exposures and scattered large stone blocks.

As no local meteorological data are available, interpolations of observed data (AD 1950–2000) from closest weather stations provides estimates at sub 1 km resolution (Hijmans et al., 2005). Analysis of the meteorological dataset reveals dry season (June–August) precipitation averages 13 mm month<sup>-1</sup> which increases to 138 mm month<sup>-1</sup> during the wet season (January–March). Mean temperature varies from 4.5°C to 7.6°C for the wet and dry season respectively. Total annual precipitation was estimated at 772 mm. Kessler (2002b) reports that additional humidity is contributed by the condensation of dew and fog, especially between 1600–3400 m asl. Our own observations at LKKU show that even during the dry season, cloud gradually ascends from the valleys to the northwest, depositing moisture on the sparsely vegetated slopes up to 4200 m asl (Figure 5.2A). Temperature ranges recorded at 3850 and 4050 m asl during September 2003, yielded values of -1.7 to 6.1°C (mean 1.8°C), and -2.3 to 9.5°C (mean 1.7°C) respectively (Hertel et al., 2008). These results indicate a lapse rate of ~4.5°C 1000 m<sup>-1</sup>, a value similar to those previously calculated elsewhere in the Andes (~6°C 1000 m<sup>-1</sup>; Baker et al., 2003).



**Figure 5.1** Map of the study site, Laguna Khomer Kocha Upper, Bolivia. **A)** Cochabamba Basin with elevations and study area marked. Modified from (Sánchez C., 2008). Inset map locates Cochabamba Basin within Bolivia and marks location of other records discussed in the text. **B)** Local features of the Laguna Khomer Kocha area including roads, watercourses and mountain ranges shown. Contour lines at 200 m intervals. **C)** Khomer Kocha Lagunas (upper and lower). Local terrain, investigated *Polylepis* woodlands and lake inputs/outflows shown. Contour lines at 20 m intervals.

The lagunas of Khomer Kocha lie in a region of rapid ecosystem changes in association with elevation. With such steep elevation gradients present in the San Mateo Valley, biogeography and vegetation is complex. Based on Bolivian classification, the lakes lie within in the sub-humid Puna and transitional Punean woodlands that split the Puna and Yungas zones along the Cochabamba section of the Eastern Cordillera (Ibisch et al., 2003; Navarro and Ferreira, 2007; Navarro and Maldonado, 2002).



**Figure 5.2** Laguna Khomer Kocha Upper and surrounding landscape. Features discussed in the text are marked and lake dimensions are displays. Viewpoint of photographs shown in Figure 5.1C. **A)** View of Laguna Khomer Kocha Upper from above looking east. Photograph taken 27<sup>th</sup> June, 2007 by J.J.Williams. **B)** View of Laguna Khomer Kocha Upper from above looking northeast. Photograph taken 17<sup>th</sup> June, 2007 by W.D.Gosling.

Today the landscape immediately surrounding LKKU is dominated by Andean grassland (Figure 5.2A and B), within which are pockets of woodland dominated by the tree *Polylepis* (Rosaceae). Kessler (2002a) implied that the relationship between grassland and woodland ecosystems is strongly influenced by human practices and that intensive land-use has severely limited *Polylepis* woodland distribution today (Ellenberg, 1958; Fjeldså and Kessler, 1996). However, the nature and degree to which humans ultimately govern the ecology of this region remains unclear and recent research has highlighted the vulnerability of these Andean woodlands solely to climatic changes (Gosling et al., 2009).

Today, two *Polylepis* woodland patches are in close proximity to LKKU (Figure 5.1C). One stand, 300 m to the north, was located at the base of an exposed rock face amongst a scree and boulder field. The second was found in the gully below LKKU. Further *Polylepis* woodland patches are also located at 3650 (*P. lanata*), 3800 and 4050 (*P. pepeii*) m asl (Hertel et al., 2008).

Today there is minimal sign of human impact at LKKU. Examination of the *Polylepis* woodland patches surrounding the lake revealed no indications of exploitation. At lower elevations (<4000 m asl) minimal human impact was also observed, although in August 2003 the grassland around the lower lake showed evidence of recent burning (Hertel et al., 2008; D. Hertel, 2010, pers.coms.). One small rock shelter and seven semi-wild horses were found near the track. The nearest agricultural fields were ~15 km away by road. Although there are remains of Inca sites regionally (e.g. Inkachaca 15 km west, >2000 m lower elevation), there is no direct route to the lake because of the steep topography.

#### **5.4) Material and methods**

A sedimentary succession 413 cm long was extracted from the deepest point in LKKU during the 2007 dry season using a cam-modified Livingstone piston corer (Colinvaux et al., 1999; Appendix A1; Plate A1.2). The deepest point was chosen to maximize sediment recovery and reduce the chances of encountering a sediment gap caused by any periods of reduced lake area. Two sediment cores (KKU-A and KKU-B) were recovered with staggered, overlapping, starting depths below the sediment-water interface (8 cm and 40 cm). The overlap ensured that a continuous record was recovered despite potential loss from core tube ends. Sediments cores were recovered in aluminium tubes (50 or 38 mm diameter, 1 m long) and sealed on site. Due to the fluid nature of the uppermost sediments, the sediment-water interface could not be recovered. The sediments were flown to the UK and stored at 4°C in The Open University cold store. The cores were split, digitally photographed and described following the Troels-Smith system (Birks and Birks, 1980) and Munsell Soil Colour Charts (2000). See Appendix A1.1 and Table A1.1 and A1.2 for description methodology and key.



The sediment chronology was based on  $^{14}\text{C}$  accelerator mass spectrometry (AMS) dating of three bulk sediment samples and five samples of charcoal fragments. All samples were submitted to NERC Radiocarbon (Environment) and analysed at the SUERC AMS Facility, East Kilbride (see Freeman et al., 2007). Samples were digested using an acid–alkali–acid pre-treatment (2 M HCl, 80°C, 2 h; 1 M KOH 80°C, 2 h; 1 M HCl 80°C, 2 h) then rinsed free of acid, dried and homogenised. The total carbon in a known weight of the pre-treated sample was recovered as  $\text{CO}_2$  by heating with CuO in a sealed quartz tube. The gas was converted to graphite by Fe/Zn reduction. All samples were pre-treated and prepared to  $\text{CO}_2$  in the same way but SUERC-32101 and 32102 contained <500  $\mu\text{gC}$  and required AMS analysis at low current. Radiocarbon dates <11 ka were calibrated using CALIB 6.01 and the SHCal04 Southern Hemisphere data set (McCormac et al., 2004; Stuiver and Reimer, 1993; 2010). Dates >11 ka were calibrated using the Fairbanks Calibration Curve (Fairbanks et al., 2005). Mean age values of the largest probability at 2 sigma were used to create the age model, with linear interpolation between dates and for the top and basal sediments. Cores KCU-A and KCU-B were matched using changes in the sediment units and banding patterns.

For physical and chemical analysis, samples were taken every 5 cm, dried for 7 days at 30°C and ground with an agate mortar and pestle. Colour properties were analyzed using a Canon LiDe flatbed scanner and the software ImageJ (Rasband, 1997-2009). Separate readings for red (R), green (G) and blue (B) colour intensities were recorded but after analysis, all three showed similar variance so a mean red, green and blue (RGB) value was used (Section 3.6.2). Total organic carbon (TOC), calcium carbonate ( $\text{CaCO}_3$ ), nitrogen (N) and sulphur (S) were determined using a LECO CNS-2000 elemental analyzer (Section 3.6.3; Appendix A2.7). The magnetic susceptibility (MS) of each sample was measured using a Bartington Dual Frequency Sensor (MS2B), corrected for mass differences (Section 3.6.1).

Cores were subsampled at 1  $\text{cm}^3$  for charcoal, pollen and fungal spore analysis at, where possible, identical sampling depths and resolution. For charcoal analysis, samples were deflocculated using 10% potassium hydroxide (KOH) for 24 hours before being sieved and separated into two size fractions >180  $\mu\text{m}$  and 100–179  $\mu\text{m}$  (Appendix A2.5). Samples



were then suspended in water on a gridded petri dish and were counted using a binocular microscope (Olympus SZX12) at  $\times 12.5$ – $25$  magnification. Charcoal abundance is represented as particulates  $\text{cm}^{-3}$ .

For pollen and spore analysis, samples were first spiked with microspheres, for concentration calculation, and then prepared using standard methods (Faegri and Iversen, 1989; Appendix A2.4). Samples were mounted in glycerol and pollen was identified using a Nikon Eclipse 50i microscope at  $\times 400$ – $1000$  magnification. A minimum of 300 fossil terrestrial pollen grains were analyzed in each sample or, where concentration was extremely low, counting was continued until 3000 microspheres had been recorded *i.e.* sample concentrations were confirmed to be below 5500 terrestrial pollen grains/ $\text{cm}^3$  (barren). Percentage values for aquatic taxa, the spores and algae were calculated relative to the pollen sum and their own abundance. Pollen grains and spores were identified using The Open University pollen reference collection, the Neotropical Pollen Database (Bush and Weng, 2006) and pollen keys (Hooghiemstra, 1984; Roubik and Moreno, 1991). All pollen and spore types recorded were described and digitally photographed for reference purposes (Appendix A4: Enclosure CD1). All data sets were entered as EXCEL spreadsheet files and converted using WinTran V1.4. Diagrams were plotted using C2 (Juggins, 2002; Juggins, 2003). Ordination analysis was run in PC-ORD v5.0 (McCune and Mefford, 2006). See Appendix A3.3.4 for the full list of ordination data.

## **5.5) Results**

### **5.5.1) Chronology and sediment description**

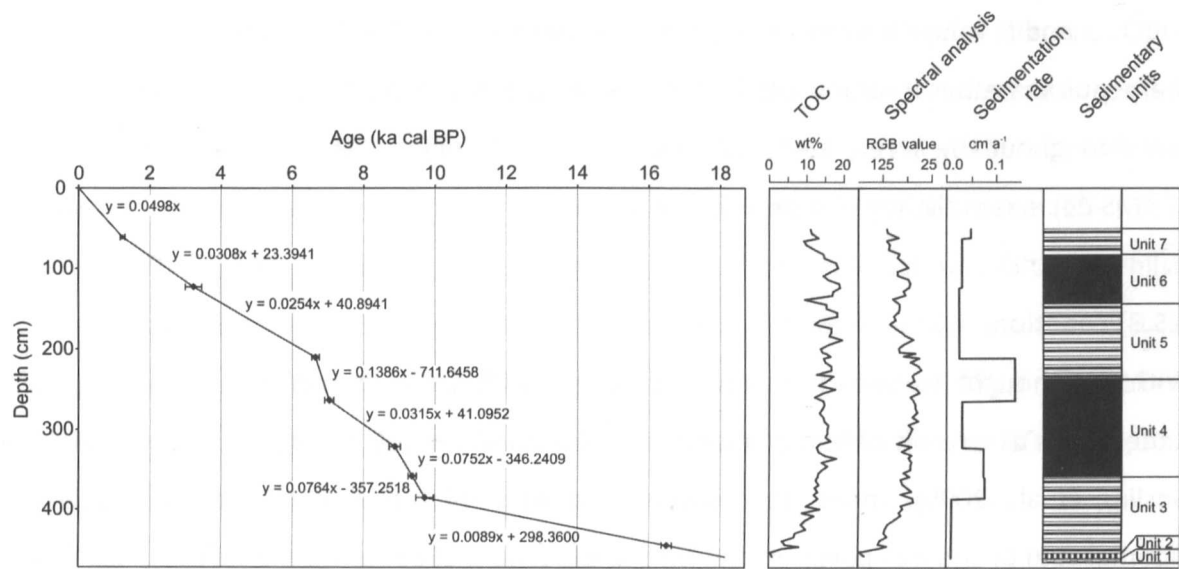
Eight  $^{14}\text{C}$  AMS dates have been used to establish the LKKU chronology (Table 5.1). Radiocarbon ages and inspection of the sediments revealed that there were no significant breaks in deposition since the inception of the lake at c. 18 ka cal BP, and that the last c. 950 years (top 47 cm) of sediment had not been recovered. Assuming no hiatuses, the age-depth model (Figure 5.3) suggests accelerated sediment accumulation rates during the early to middle Holocene (c. 10–6.5 ka cal BP).

Laboratory code	Depth (cm)	Description	<sup>14</sup> C Age (yr BP $\pm$ 1 $\sigma$ )	Cal. Range (cal yr BP)
SUERC-22356	61.5	Bulk sediment	1359 $\pm$ 37	1148 – 1300
SUERC-32101	123	Charcoal fragments	3123 $\pm$ 89	2998 – 3461
SUERC-31725	210	Charcoal fragments	5910 $\pm$ 38	6545 – 6783
SUERC-31726	263	Charcoal fragments	6190 $\pm$ 38	6906 – 7162
SUERC-22357	321	Bulk sediment	8086 $\pm$ 41	8661 - 9029
SUERC-31727	358	Charcoal fragments	8400 $\pm$ 40	9149 - 9479
SUERC-32102	385	Charcoal fragments	8727 $\pm$ 125	9472 - 10153
SUERC-22358	445.5	Bulk sediment	14112 $\pm$ 61	16363 - 16645

**Table 5.1** Radiocarbon dates and calibrated ages for Laguna Khomer Kocha Upper cores. Calibration determined using CALIB 6.01 and the SHCal04 dataset for dates <11 ka (McCormac et al., 2004; Stuiver and Reimer, 1993; 2010). Dates >11 ka were calibrated using the Fairbanks Calibration Curve (Fairbanks et al., 2005).

The 413 cm core was divided into seven basic sedimentary units (Figure 5.3). Unit 1 comprises greenish-gray clays (460–455.5 cm, c. 18.1–17.6 ka cal BP). Unit 2, (455.5–449.5 cm, c. 17.6–16.9 ka cal BP) consists of light brown very coarse sandy sediment. Unit 3 (449.5–360 cm, c. 16.9–9.4 ka cal BP) comprises pale strongly banded sandy deposits between gyttjas. The bands are up to 1 cm with gradual to sharp boundaries. Banding becomes less prominent and gyttjas darker brown in colour towards the upper boundary of this zone as the quantities of sandy material reduces. Unit 4 (360–219 cm, c. 9.4–6.7 ka cal BP) comprises dark brown gyttjas with a jelly-like consistency. Unit 5 (219–133 cm, c. 6.7–3.6 ka cal BP), contains dark grey gyttjas with some frequent, broad (1–2 cm) bands of darker gyttjas with gradational boundaries. In unit 6, 133–77cm, (c. 3.6–1.7 ka cal BP) banding is reduced and the sediments return to dark brown gyttjas similar to that of unit 4. The uppermost unit, 7, begins at 77 cm (c. 1.7 ka cal BP) and consists of very dark brown gyttjas, but with some strong banding evident similar to that of zone 5. The material of this zone is very jelly-like once again. Sediments

upwards of 47 cm below the sediment-water interface were not captured. These sediments were extremely fluid in nature and could not be extracted with the coring apparatus available, despite numerous attempts.



**Figure 5.3** Age-depth model, physical and chemical properties and lithology of Laguna Khomer Kocha Upper sediment cores. Details of  $^{14}\text{C}$  dates given in Table 1. The sedimentary units are described in main text. Sediments above 47 cm were not retrieved due to their extremely fluid nature. Total organic carbon (TOC) plotted against depth in Figure 5.6. Wt% = weight percent. RGB = mean value of red, green and blue color intensities. Spectral analysis axis is inverted.

### 5.5.2) Physical and chemical properties

Spectral properties are often controlled by organic content (Nederbragt et al., 2006), and analysis of the LKKU cores revealed that the RGB colour values and TOC show similar, but opposite overall trends, particularly in the oldest sediments (Figure 5.3). From the base of the core to 298 cm (c. 8.1 ka cal BP), RGB values show an overall decreasing trend (170 to 65) and TOC values gradually increase from 0 to 16 wt%. Small-scale variations, more pronounced in TOC than RGB, are apparent.

From 298 to 208 cm (c. 8.1–6.6 ka cal BP) RGB values remain low (<75), before generally higher values with increased fluctuation (60–117) are recorded during the last 6 ka years. In the TOC record, values remain generally high from 298 cm, with a mean value of 15

wt%. Superimposed on this are four maxima in TOC, where values peak at >17 wt% (95, 123, 155 and 188 cm) with a c. 900–1300 year periodicity. The RGB analysis shows the same trends as the TOC data, but the signal is less pronounced. From 2.3 ka cal BP, TOC (and RGB) values show an overall declining (increasing) trend.

CaCO<sub>3</sub>, S and N values are low throughout the entire core (<3 wt%, Figure 5.6). Except for the penultimate basal sample (453cm, c. 7.3 ka cal BP; 134.7 SI units), MS values remain low throughout the core (-8.3 to 9.6, mean of -0.77 SI units). After 207 cm (c. 6.5 ka cal BP) MS decreases slightly (Figure 5.6).

### 5.5.3) Zonation

With fire thought to be a transformative agent within the ecosystems of the tropical Andes, both as a result of human practices and natural climatic forcing (Bush et al., 2010; Gosling et al., 2009), zones were determined with reference to charcoal abundance. Optimal sum of squares partitioning (Birks and Gordon, 1985) using the software ZONE v. 1.2 (Lotter and Juggins, 1991) was performed on charcoal particulate counts to guide the position of zone boundaries. Four Khomer Kocha Upper fire stratigraphic zones were identified: KKU-F1, KKU-F2, KKU-3 and KKU-F4 (Figure 5.4).

### 5.5.4) Pollen, spore and charcoal description

*KKU-F1. 460–428 cm (18,130–14,541 cal yr BP). 5 charcoal samples, 4 pollen samples.*

Zone KKU-F1 is defined by very low total charcoal abundances throughout (<25 particulates cm<sup>-3</sup>; Figure 5.4B). The pollen record (Figure 5.4A) shows *Polylepis/Acaena* pollen as a major component of the assemblage (up to 10%). The montane forest taxa *Podocarpus* and *Hedyosmum*, also reach maximum individual values for the entire record (up to 6% and 8% respectively). Poaceae, although a major component throughout the entire pollen record (>20%), fluctuates between ~30–60%. Excluding the penultimate basal sample, which had very low pollen concentration (1400 grains cm<sup>-3</sup>), other major constituents include Moraceae/Urticaceae undiff. (10–15%), *Acalypha* (4–14%), *Asteraceae* (3–9%), *Alnus* (3–9%) and *Celtis* (<3–7%). The aquatic taxon *Isoetes* shows a significant increasing trend from the oldest sediments, reaching abundances in excess of 40%. Spores are generally high throughout the zone. In particular, samples below 443 cm,

showed significant abundances of monolete (20–10%) and trilete (10%) spores, and the dung fungus *Sporormiella* (3%). Fossil pollen concentration is low prior to 16.2 ka cal BP ( $<160,000$  grains  $\text{cm}^{-3}$ ), but subsequently increases to  $>550,000$  grains  $\text{cm}^{-3}$ .

*KKU-F2. 428–389.5 cm (14,541–10,166 cal yr BP). 4 charcoal samples, 4 pollen samples.*

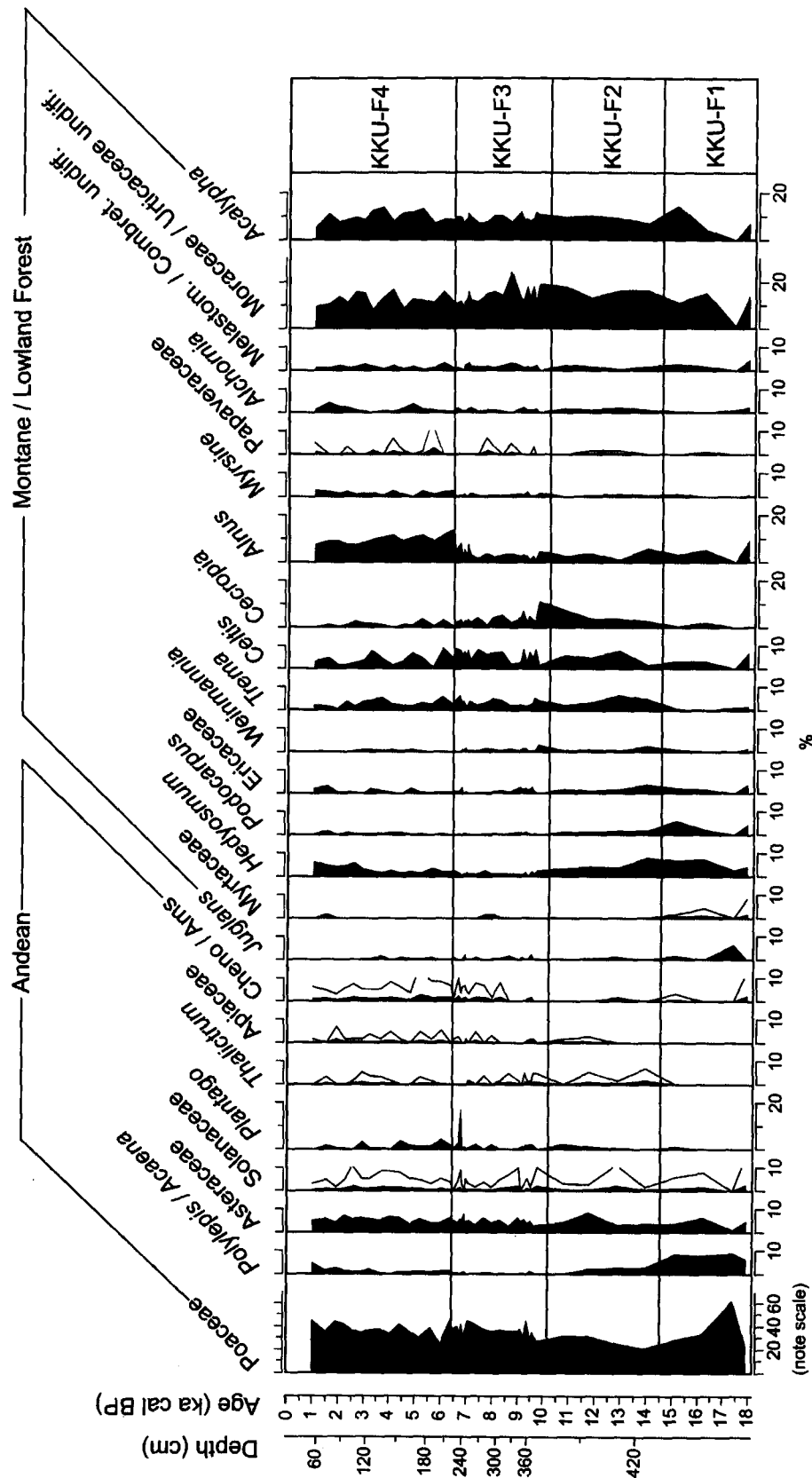
A marked increase in the abundance of charcoal fragments (65–125 particulates  $\text{cm}^{-3}$ ) is evident throughout K KU-F2 (Figure 5.4B). *Polylepis/Acaena* and *Podocarpus* pollen declines in abundance by at least half, reaching low values ( $<1\%$ ) at the upper zone boundary (Figure 5.4A). Poaceae are highly abundant throughout this zone (20–32%). *Cecropia* (3–7%) and *Trema* (2–7%) become important components during K KU-F2, whilst the abundance of *Hedyosmum* declines to below 3%. *Isoëtes* shows increasing, but fluctuating, abundance (30–65%), peaking at 394 cm (c. 10.7 ka cal BP). Fossil pollen concentration shows a similar trend to *Isoëtes* with values between 430,000–1,800,000 grains  $\text{cm}^{-3}$  (Figure 5.4B).

*KKU-F3. 389.5–204 cm (10,166–6415 cal yr BP). 21 charcoal samples, 19 pollen samples.*

Charcoal abundances show a high level of change throughout zone K KU-F3, ranging from 100–1000 particulates  $\text{cm}^{-3}$ , with peaks at 385, 320, 253 and 210 cm. The scale of these oscillations is a unique feature of zone K KU-F3. After 385 cm (9.7 ka cal BP) *Cecropia* pollen decreases in abundances by more than half to between 1–7%. A further decline in *Hedyosmum* is also evident ( $<2.5\%$ ), whilst the abundance of *Polylepis/Acaena* pollen remains at very low values throughout ( $<1\%$ ). From 303 cm (c. 8.3 ka cal BP) to the upper most sediments, Chenopodiaceae/Amaranthaceae (Cheno/Ams) becomes a small, but persistent, constituent of pollen assemblage ( $<2.5\%$ ). Poaceae abundances increase (30–45%) and a peak in *Plantago* (16%) is evident at 225 cm (c. 6.8 ka cal BP). *Isoëtes* has fluctuating abundances (25–70%), with minimum values recorded at 308 and 225 cm (Figure 5.4B and 5.6). A peak in *Isoëtes* occurs between 283–253 cm (c. 7.7–7.0 ka cal BP), which is simultaneous with a peak in *Sporormiella* (3–7%) and in both charcoal size fragments. Although present in previous zones, the green alga *Pediastrum* becomes an increasingly important component of the sediment record (up to 8%) during K KU-F3. Fossil pollen concentrations show high frequency and high amplitude variation (230,000–1,500,000 grains  $\text{cm}^{-3}$ ).

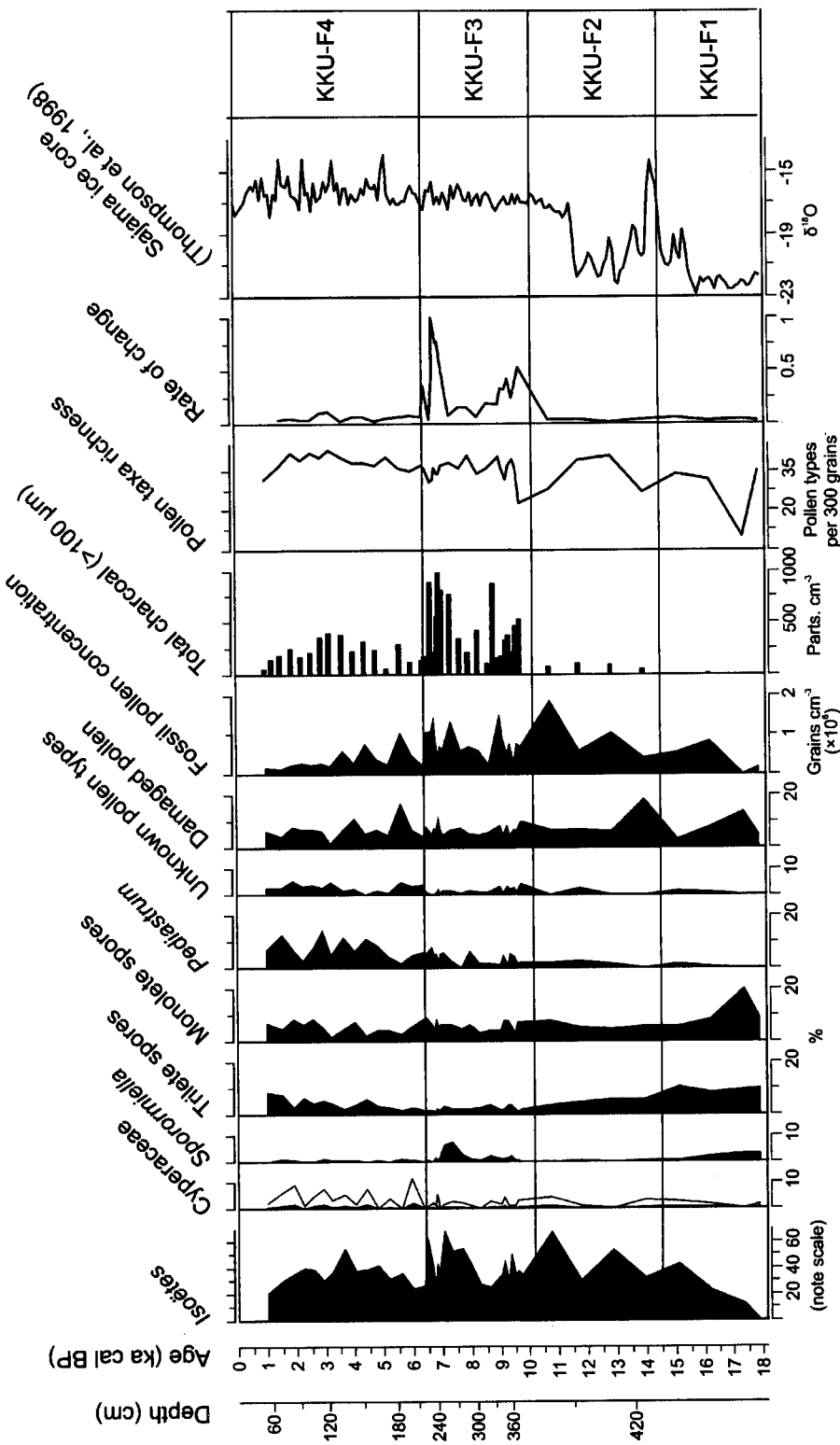
*KKU-F4. 204–47cm (c. 6415–944 cal yr BP). 16 charcoal samples, 15 pollen samples.*

Charcoal particulates increase from 204 cm, peaking at 418 particulates  $\text{cm}^{-3}$  at 123 cm (c. 3.2 ka cal BP). Charcoal then decreases towards the uppermost sediments (Figure 5.4B). The pollen assemblage is characterised by an increased *Alnus* abundance (7–13%). Poaceae values are equivalent to those of the previous zone (KKU-F3), but with slightly increased variation (25–45%). During the zone, *Polylepis/Acaena* and *Hedyosmum* gradually increase, reaching values of 5% and 6% respectively by the uppermost sample (51 cm). *Myrsine* abundance increases throughout the zone (up to 3%), and sporadic occurrences of *Alchornea* and *Plantago* (both <4%) are also evident. *Isoëtes* shows an increasing trend prior to 133 cm (55%), followed by a decrease towards the more modern sediments (20%). For the first time, Cyperaceae reaches values >1% and an increase in *Pediastrum* (up to 14%) marks its highest abundance in the record. Fossil pollen concentrations show high frequency and high amplitude variation but with an overall decreasing trend towards more recent sediments (150,000–1,000,000 grains  $\text{cm}^{-3}$ ).



**Figure 5.4A)** Percentage diagram of terrestrial pollen taxa. Taxa are grouped based on the vegetation descriptions of Navarro and Maldonado (2002), Reese and Lui (2005) and Ortuño et al. (2011) Thin lines applied to taxa with low percentage values represent a 5x exaggeration of actual values. The fire zones (KKU-F1, 2, 3 and 4) discussed in text are shown.

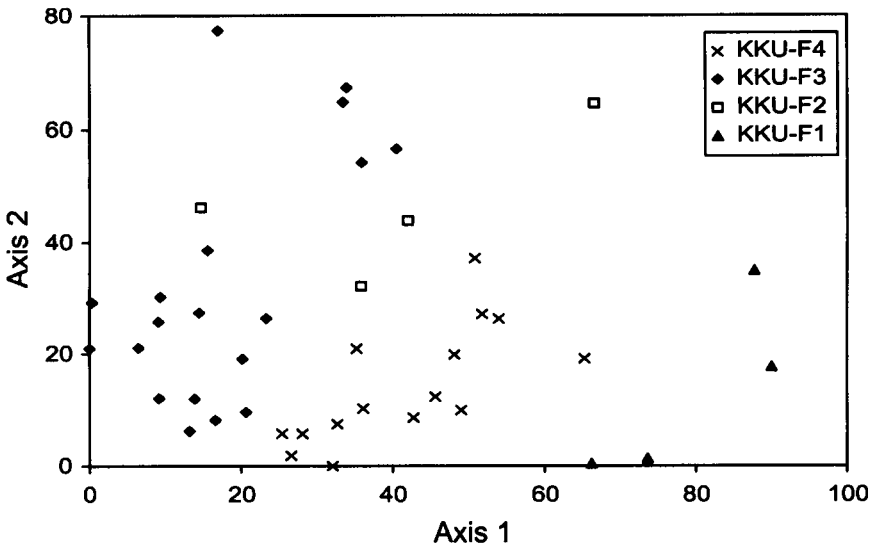




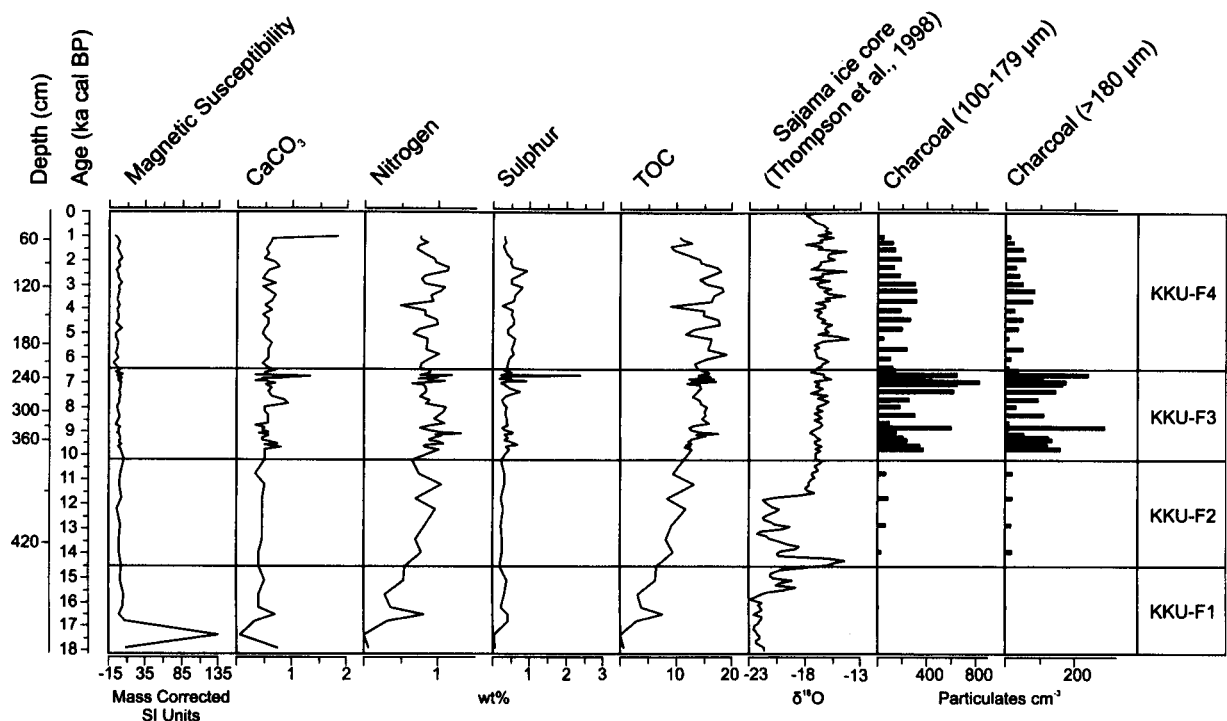
**Figure 5.4B)** Percentage diagram of aquatic taxa, spores and algae. Percentage values calculated relative to the pollen sum and their own group abundance. Thin lines applied to taxa with low percentage values represent a 5x exaggeration of actual values. Total pollen concentration and total charcoal particulates also shown per cm<sup>3</sup>. Pollen taxon richness is the number of unique pollen types identified from within the pollen sum count (300). Rate of change analysis is calculated from the Euclidean distance between adjacent sample scores in the first 3 DCA axes then divided by the intersample time (following Urrego et al., 2009). Sajama δ<sup>18</sup>O ice core record is also shown (Thompson et al., 2000). The fire zones (KKU-F1, 2, 3 and 4) discussed in text are shown.

5.5.5) Ordination

Detrended correspondence analysis (DCA) explored trends within the terrestrial pollen assemblage. A rescaled solution of the first 3 axes was returned with rare taxa downweighted. Sample scores for axis 1 and 2 are plotted showing KKU fire zones (Figure 5.5). The rate of change (ROC) is calculated from the Euclidean distance between adjacent samples from the 3 DCA axes then divided by the intersample time (following Urrego et al., 2009). The results suggest that the biggest change occurred during, and on the boundary transitions of zone KKU-F3 (Figure 5.4B).



**Figure 5.5** Results of sample scores for the DCA (Axis 1 and 2) ordination analysis. The different symbols refer to the different fire zones.



**Figure 5.6** Physical and chemical properties and charcoal abundance of Laguna Khomer Kocha Upper sediment cores plotted against age. Wt% = weight percent. The fire zones (KKU-F1, 2, 3 and 4) discussed in text are shown.

## 5.6) Environmental reconstruction and discussion

### 5.6.1) Deglacial vegetation dynamics

Rising regional temperatures and associated deglaciation following the LGM is recorded in ice core data from the central Andes (Thompson et al., 2000). In the relatively wet Eastern Cordillera, glacial modelling suggests that temperature changes were ultimately controlling glacial dynamics during the LGM and deglaciation period (Kull et al., 2008; Zech et al., 2007). By c. 18 ka cal BP, warming had allowed the formation of an increasingly ice-free and deeper water body at LKKU. Sedimentation rates are low (<0.01 cm yr<sup>-1</sup>) probably reflecting the minimal in-wash of free organic material (e.g. charcoal) and the low turnover in the terrestrial taxa, as shown by the ROC analysis (Figure 5.4B). Increased MS and low TOC (Figure 5.3 and 5.6) represent a period of reduced productivity, and there were large inputs of sandy material from the unstable and erosive slopes above the lake. Pollen grain concentration is initially low, probably due to poor preservation of grains. Conversely, spore producing plants, which are early colonisers and

more robust to oxidation, are a relatively more important component of the late glacial assemblage (Figure 5.4B).

The abundance of *Sporormiella* fungal spores indicates the early presence of herbivores and suggests a shallow lake at this time. *Sporormiella* is a coprophilous ascomycete fungus common on the dung of herbivores (Ahmed and Cain, 1972). Although a useful proxy to indicate increased natural herbivore density (Davis and Shafer, 2006; Gill et al., 2009) and livestock intensification (Davis et al., 1977; Chapter 4; Williams et al., 2011:). *Sporormiella* also has a strong positive relationship with proximity to shoreline due to its poor dispersal (Raper and Bush, 2009). At LKKU we suggest that a decreased lake depth and surface area gave herbivores access towards the more central section of the lake, thus closer to the coring site, increasing spore abundance in the sediment record.

*Isoëtes* is associated with shallow, cool water (Navarro and Maldonado, 2002), and is indicative of water levels <4 m (Bush et al., 2005; Urrego et al., 2011). However, *Isoëtes* is unable to survive persistent freezing water (Dejoux and Iltis, 1992). Therefore the low abundance of *Isoëtes* in the LKKU record prior to c. 16.9 ka cal BP probably indicates a relatively shallow lake subjected to regular hard freezes (Figure 5.4B). This interpretation is consistent with local glacial modelling which suggests ~6–7°C cooling compared to modern during the LGM (Kull et al., 2008). A decrease in *Sporormiella* from c. 16.2 ka cal BP, suggests a deepening of the lake at this time as animals are restricted from the central portion of the lake. Although we interpret low water levels at LKKU between c. 18.1–16.2 ka cal BP, this is not necessarily evidence of reduced precipitation but more likely a result of moisture locked up as ice.

Prior to c. 14.5 ka cal BP fire was virtually absent from the landscape surrounding LKKU (Figure 5.4B). Within warming, but relatively moist surroundings free from fire, *Polylepis* woodland was a major component of the local landscape, more abundant than any other time over the past 18 ka years (up to 10%). Although *Polylepis/Acaena* pollen cannot be easily separated, it is most likely that the pollen recorded here is predominantly *Polylepis* rather than from *Acaena*. *Acaena* is today present in warm humid valleys and the pollen is has not been identified as capable of long-distance transporter (Ortuño et al., 2011).

Comparison to reference pollen material of several *Polylepis* species examined at the Herbario Nacional Martín Cardenas, Cochabamba, reveals close morphological similarities to the fossil *Polylepis/Acaena* types identified from LKKU.

The data from LKKU shows that although attaining relatively high abundances, *Polylepis/Acaena* pollen never reached sufficiently high values to indicate complete coverage of the landscape surrounding LKKU. At lakes surrounded by *Polylepis* woodland, pollen in sediment cores is typically >30% (Hanselman et al., 2011; B. Guido, 2011, pers. coms.). Although undoubtedly more extensive than the modern local distribution on scree slopes and gullies, *Polylepis* woodland remained, as today, in patches within an environment dominated by Andean grassland. The palaeoecological record from the Refugio lakes (800 km northwest, 3400 m asl; eastern Peruvian Andes; Figure 5.1A) reveals that during a similar time of minimal burning, *Polylepis* woodland was also locally abundant (~20%), but in contrast to LKKU, grassland was reduced and replaced by montane forest taxa such as *Hedyosmum* and *Vallea* (Urrego et al., 2011).

The long-distance transport of pollen in the Andes has already been observed (e.g. Ortuño et al., 2011; Reese, 2003; Reese and Liu, 2005; Weng et al., 2004). At LKKU, upslope wind provides a background signal of vegetation dynamics at lower elevations throughout the record. The pollen assemblage suggests that warming temperatures and moist conditions between c. 18–14.5 ka cal BP facilitated the expansion of montane forest vegetation upslope (e.g. *Podocarpus*, *Hedyosmum*, *Juglans*) in agreement with other palaeoecological data (e.g. Urrego et al., 2010).

The local presence of fire at LKKU from c. 14.5 ka cal BP, although minimal, altered the vegetation composition. Although there is no apparent temperature response in the pollen data, the onset of burning at this time does coincide with a peak in temperatures and aridity suggested in the Sajama ice core record (Thompson et al., 2000; see Figure 5.4B). This is also broadly concomitant with demise of palaeolake Tauca, on the Altiplano (Argollo and Mourguiart, 2000; Baker et al., 2001a; Sylvestre et al., 1999). The Tauca highstand (c. 18–14 ka BP), perhaps related to Heinrich 1, is associated with cold and wet conditions that persisted in much of the southern Andes (Blard et al., 2009). An increase

in the occurrence of fire was also seen at c. 14.5 ka cal BP at Lake Titicaca (Paduano et al., 2003). These authors associate fire to increased fuel load, but considering the abundance of locally sourced pollen in the records at LKKU before the onset of burning, we do not interpret fuel load deficit prior to c. 14.5 ka cal BP to be the main cause of minimal burning on the Andean flank. Therefore, we suggest a climatic trigger (warming and drying) for the onset of burning. The impact of fire was immediately apparent on the high Andean vegetation because the data indicates that *Polylepis* woodland was reduced by two thirds of its previous abundance, as fire removed it from the most readily burnt, flatter areas around the lake which were surrounded by grasses and offered no fire protection (*i.e.* scree slopes) (Figure 5.4A).

The pollen data from LKKU supports conclusions drawn from fossil pollen records at lower elevation sites in the eastern Andes (e.g. Urrego et al., 2011). These data suggest that low elevation montane forests are also sensitive to changes in net moisture (temperature/precipitation) and burning during the deglaciation period. Montane *Podocarpus* and *Hedyosmum* both decline, while lowland *Trema cf. micrantha* and *Cecropia* increase as landscape disturbance, probably resulting from fire, intensified. This almost simultaneous response of vegetation from different biogeographical zones suggests that while each fire event was localised, the underlying driver of the frequency and intensity of burning was regional climate.

The LKKU pollen assemblage reveals a unidirectional transition in vegetation following the LGM, influenced by increasing fire occurrence. There are no apparent reversals to suggest a response to an interstadial or Younger Dryas-type stadial event, which has been seen in the Sajama ice core (Figure 5.4B: Thompson et al., 1998). Surface exposure dating of glacial moraines indicates that the last period of glacial advances around Cochabamba occurred at c. 11 ka cal BP (Zech et al., 2007). However, the failure to detect such events in the LKKU record may be a result of the sampling resolution for pollen being too coarse throughout this section.

### 5.6.2) Early and mid-Holocene climate variation

At the onset of the Holocene, the ecosystems of the eastern Andes become less constrained by the large-scale regional temperature changes (such as those recorded in the Sajama isotope record; Figure 5.4B), and show greater response and sensitivity to variation in net moisture availability. From 10.7–9.7 ka cal BP, fire frequency and intensity increased markedly once again, indicated by more than doubling of the charcoal particulate counts (Figure 5.4B). ROC analysis reveals that the turnover of terrestrial taxa at this time was greater than before (Figure 5.4B). Poaceae increased in dominance in comparison to *Polylepis* woodland (Figure 5.4A), as the aridity led to increased flammability and fire intensity that was unfavourable to woodland (Gosling et al., 2009). Between c. 10.7–6.4 ka cal BP, *Polylepis/Acaena* pollen remained below 1% or was completely absent. However, *Polylepis* pollen does not transport far (Salgado-Labouriau et al., 1977), and therefore its persistence in the majority of samples suggests *Polylepis* remained locally present; possibly limited to small isolated pockets on the scree slopes, which act as natural fire breaks. A similar decline in *Polylepis* woodland has been observed at Lake Siberia (2920 m asl; Figure 5.1A), which today is within Andean cloud forest. The pollen record indicates that by c. 11 ka cal BP, *Polylepis* pollen at Siberia declined from >10% to zero, while a simultaneous rise in the frequency of micro-charcoal fragments indicated a intensification of burning (Mourguiart and Ledru, 2003).

At LKKU, the increased aridity and intensified burning led to large declines in several montane forests elements (e.g. *Podocarpus* and *Hedyosmum*) during the early to mid-Holocene. If increasingly warmer temperatures had occurred during this time, this would have facilitated the upslope migration of lowland taxa, as per the classic view of species movement in warmer conditions. However, the decline in montane forest elements suggests that aridity prevented this vegetation response, and supports similar interpretations at Lake Titicaca (Bush et al., 2010). Fire therefore became a key transformer of the vegetation composition, limiting the range of the montane forests.

An initial detrimental impact of fire on plant diversity around the LKKU ecosystem is apparent from the decline in the total number of pollen taxa from >35 to <25 following the onset of burning at c. 10 ka cal BP. However, species richness recovers (>35 taxa)



within c. 100 years, and remains high in the new fire-dominated ecosystem. The impact on some taxa (e.g. *Celtis*, *Trema* and *Weinmannia*) is less than on other lowland forest trees (Figure 5.4A). This may be due to their preference for more open, arid or warmer conditions. The small, but persistent, occurrence of Cheno/Ams in the pollen assemblage from c. 8.3 ka cal BP suggests conditions had become favourable for vegetation generally preferring dry, disturbed landscapes. Increased aridity between c. 9.6–6.7 ka cal BP is also revealed in the spore assemblage. Increased *Sporormiella* fungal spores probably indicate lower water-levels, as herbivores are able to access more of the lake (Raper and Bush, 2009) or, perhaps, more animals visit LKKU as other local water bodies dry up.

This phase of increased aridity at LKKU during the early to mid Holocene is concomitant with a regional decrease in precipitation and reduced lake levels identified in numerous records across the Andes and Amazonia (Bush et al., 2010). Although varying in intensity and timing spatially, the Holocene dry event (HDE) is understood to be a drought of multi-millennial scale, but was punctuated with episodic wet events (Abbott et al., 2003; Bush et al., 2005; Grosjean, 2001; Hillyer et al., 2009; Paduano et al., 2003; Valencia et al., 2010).

The onset of the HDE caused many lakes across the Andes to either reduce in depth (e.g. Lake Titicaca; Cross et al., 2000) or completely dry out (e.g. Refugio lakes, Peru; Urrego et al., 2011). Close to LKKU (40 km southeast), although in an inter-Andean setting, the record of Lake Challacaba (Vacas Lake District, 3400 m asl; Figure 5.1A) also indicates desiccation of the lake basin prior to c. 4 ka cal BP (Chapter 4; Williams et al., 2011). However at LKKU, despite a lowering of the lake level, sediments were continually deposited throughout the height of the HDE as indicated by the presence of *Pediastrum* in all samples (Figure 5.4B). With evidence suggesting that precipitation was reduced and/or temperatures increased during this period, an explanation for the continued presence of water at LKKU is necessary. We consider that a continuation of ground-level cloud regularly covered the site as is common in the eastern Andes (Kessler, 2002b), and was observed during dry season fieldwork (Figure 5.2A). We suggest that this moisture supply, in addition to precipitation, was fundamental in maintaining an inundated lake basin. This finding is in contrast to those from the Refugio lakes where the authors report cloud

cover was insufficient to maintain the presence of open water bodies (Urrego et al., 2011). However, the Refugio lakes are today shallower than LKKU (1.5–0.5 m less), and so more susceptible to complete desiccation. While it is likely that ground-level cloud was reduced during the HDE at LKKU, it was sufficient to maintain the lake by reducing UV exposure (evaporation) and continuing to supply moisture during periods of reduced precipitation.

In the LKKU record we interpret simultaneous peaks in *Sporormiella*, Poaceae, charcoal and *Isoëtes* as indicating that greatest drought intensity occurred between c. 7.3–7 ka cal BP. The timing of aridity concurs with evidence for Holocene drought across the Peruvian/Bolivian Andes, ranging from low elevation slopes to the Altiplano: i) Lake Consuelo; 1360 m asl; c. 7.4–5 ka cal BP (Urrego et al., 2010), ii) Lake Pacucha 3095 m asl, c. 8.3–5 ka cal BP (Hilleyer et al., 2009), iii) Laguna de Chochos; 3285 m asl, c. 9.5–7.3 ka cal BP (Bush et al., 2005), and iv) Lake Titicaca; 3810 m asl c. 8–5.5 ka cal BP; (Baker et al., 2001b). Increased charcoal frequency in the Siberia lake record from c. 11–4.5 ka cal BP may also indicate reduced moisture availability in the region (Bush et al., 2007; Mourguiart and Ledru, 2003).

In addition to confirming that the HDE was multi-millennial in duration, the LKKU record also supports more recent findings that suggest this dry period was punctuated with episodic wet phases (e.g. Hilleyer et al., 2009). At LKKU this is indicated by: i) the non-linear direction changes in many locally growing taxa (e.g. *Plantago*), ii) high ROC scores indicating regular, large-scale, rapid terrestrial vegetation changes (Figure 5.4B), iii) high amplitude and frequency fluctuations in charcoal and *Isoëtes*, and iv) increased sedimentation rate, probably due to in-wash of material during intense period of precipitation. The increase in TOC, following onset of intensified burning from c. 10.1 ka cal BP, also suggests that the sediment being washed in had a high abundance of organic material (*i.e.* charcoal fragments). A peak in pollen of the high elevation bog taxa *Plantago* (Ortuño et al., 2011) at c. 6.8 ka cal BP either represents an increase in marsh habitat on the shores of the lake in response to lowered lake level, a situation observed at the lower lake today, perhaps resulting from the infilling of the basin adjacent to LKKU (Navarro and Maldonado, 2002), or the presence of a larger wetland habitat nearby.

### 5.6.3) Formation of the modern vegetation structure

A sharp decline in burning at c. 6.4 ka cal BP marks the end of the HDE at LKKU (Figure 5.4B). Termination of this event has been linked to a resumption of stronger ENSO activity following the “weak” El Niño regime that is thought to have dominated the mid-Holocene period (Rein et al., 2005). Concomitant with decreased burning, an increase in *Alnus* (Andean Alder) indicates increased moisture. *Alnus* is a pioneer taxon, growing in marsh and riparian transitional Punean woodland (Navarro and Maldonado, 2002). As a copious pollen producer with long-distance dispersal on upslope winds, it is present in most Andean fossil pollen records above the Andean forest treeline (Weng et al., 2004). Today *Alnus* occurs on slopes below the lower Khomer Kocha lake (<3800 m; D. Hertel, 2010, pers. coms.). It is therefore likely that the establishment of *Alnus* woodland downslope would be sufficient to provide a significant quantity of *Alnus* pollen to LKKU. The increase in *Alnus* at c. 6.4 ka cal BP indicates regionally wetter conditions. As LKKU is >600 m above the modern elevation limit of *Alnus* (Weng et al., 2004) it is unlikely that marsh-woodland ever colonised the slopes immediately surrounding the lake.

The return to wetter conditions after the HDE allowed *Polylepis* woodland to expand from the pockets in which it was restricted, suggesting that fire and climate aridity was critical in determining the niche space available for woodland growth. At Refugio, despite the return of climatically favourable conditions, the onset of human activities prevented the local expansion of *Polylepis* woodlands after the HDE (Urrego et al., 2011). The different dynamics of *Polylepis* at the two sites highlights the pitfalls in assuming all high Andean ecosystems have been impacted by humans to a similar degree. Our data suggests that it is incorrect to assume the current patchy distribution of *Polylepis* is solely the result of long-term human impacts as previously suggested (Ellenberg, 1958; Kessler, 2002a).

Fire reduction and increased precipitation at lower elevations also enabled the re-expansion of Andean and montane forest, as *Hedyosmum*, *Alchornea* and, to a lesser extent, *Myrsine* all increase in abundance. The reappearance of *Hedyosmum* at high abundance may also indicate cooler temperatures, as this taxon was also dominant during the early deglaciation period (c. 18–15 ka cal BP). Intriguingly *Cecropia* and *Podocarpus* do not appear to respond to the increased net moisture in the region.

The increasing abundance of *Pediastrum* (cf. *boryanum*) throughout KKU-F4 is difficult to interpret. The taxon is restricted to freshwater habitats (Komárek and Jankovská, 2001) and *P. boryanum* var. *longicorne* appears closest to the type found at LKKU. It is today common in high elevation, clear waters, and has a pH optimum of 7.2–7.4 (Jankovská and Komárek, 2000; Weckström et al., 2010). Therefore since *P. boryanum* became dominant in LKKU (c. 4.4 ka cal BP, >10%), pH and other lake variables have remained close to this optimum. In addition, as *Pediastrum* does not bloom in saline conditions (Woodward and Shulmeister, 2005), its presence indicates continuous freshwater, and supports the interpretation of year-round input from ground-level clouds.

#### 5.6.4) Potential anthropogenic impacts

Much discussion has focussed on the timing and impacts of past human populations across the Andes (e.g. Chepstow-Lusty et al., 1996; Coltorti et al., 2010; Dillehay, 2008; Ellenberg, 1979; Lynch, 1990; Mondini, 2002; Chapter 4; Williams et al., 2011). However, the heterogeneous nature of Andean topography, microclimatic and flora mean that it is unlikely that all locations experienced uniform patterns of human impact. Broad generalisations imply that ancient human cultures had no preference for climate, vegetation or resource potential; which the archaeological records suggests was not the case. For example, the favourable environmental conditions of the Cochabamba Basin led the Inca to cultivate maize, resulting in the area being known as the “granary” of the south central Andes (Lone and Lone, 1987; Zimmerer, 2000). In contrast, the palaeolimnological record at Lake Challacaba, just outside these favourable agricultural lands, records no occurrence of maize despite at least 4 ka of human occupation (Chapter 4; Williams et al., 2011).

Although the appearance of Chen/Ams pollen in the LKKU record from 8.3 ka cal BP could represent the cultivation of *Chenopodium quinoa*, a staple dietary component before *Zea mays*, the low abundance (<2.5%) suggests that this is unlikely, as was also inferred at Laguna de Chochos (Bush et al., 2005). At sites where human occupation is apparent from the sediment records, Chen/Ams pollen reaches much higher abundances, e.g. Marcococha (10-25%) and Pacucha (up to 51%) in the Peruvian Andes (Chepstow-Lusty et al., 2003; Valencia et al., 2010). The low (<2.5%) abundance of

Solanaceae pollen, the tubers of which are harvested, suggests they were not cultivated, and the absence of other crop pollen suggests that LKKU was not a site of human habitation.

### **5.7) Conclusions**

The sediment record of LKKU represents a continuous archive of environmental change and vegetation dynamics during the past 18 ka. The proxy data suggest a relatively gradual climatic transition from the LGM, with increasing fire occurrence. There is no evidence for an interstadial or Younger Dryas-type stadial, which is apparent in the Sajama ice core record (Thompson et al., 1998).

The correlation of vegetation change to the zones established from charcoal analysis, shows that fire, governed by climatic variation in temperature and precipitation, has long been a transformative agent in high eastern Andean ecosystems. Rate of change analysis shows that the fastest vegetational change occurred during periods of high burning frequency, associated with the Holocene drought. The record confirms that the HDE was multi-millennial in duration (c. 10.1–6.4 ka cal BP) and supports evidence that this period was punctuated by episodic wet phases. The onset of generally wetter conditions from c. 6.4 ka cal BP concurs with the timing of increased moisture at other eastern Andean locations (e.g. Refugio and Siberia), and also with most Andean and Amazonia lakes (Bush et al., 2010; Mourguiart and Ledru, 2003; Urrego et al., 2011).

The LKKU pollen record provides the first opportunity to examine the dynamics of local woodland expansion and contraction in a climatically sensitive region of the eastern Bolivian Andes. Until c. 14.5 ka cal BP, the absence of fire allowed *Polylepis* woodland to form a major component of the local environment, when it was more abundant than any other time during the past 18 ka. However, *Polylepis* woodland never completely covered the landscape surrounding LKKU and remained in patches within an Andean grassland-dominated environment. The expansion of *Polylepis* woodland after the HDE suggests that fire and aridity was critical in determining the niche space available for woodland

growth. However, these changes occurred in a landscape largely free from human pressures.

Long-distance transport of pollen on upslope winds to LKKU provides evidence of vegetation changes in the lower montane forests. These data highlight the sensitivity of the Yungas to changes in climate and burning regime, supporting the conclusions found at lower elevation sites in the eastern Peruvian Andes (Urrego et al., 2011). Simultaneous changes in both Andean and lowland taxa suggest that vegetation dynamics in the two environments can be linked to a common climatic driver.

The increase in human populations throughout the late Holocene does not appear to have impacted the environment around LKKU, highlighting the importance of the site in providing a record of vegetation response to climate without anthropogenic influence. In particular, there appears to have been no decline in the highly sought-after wood resource provided by both *Polylepis* and *Alnus*, which has been documented across much of the Andes (Chepstow-Lusty et al., 1998; Fjelds  and Kessler, 1996; Weng et al., 2004). Although LKKU has minimal human impacts, the record does not cover the last c. 1000 years when the Tiwanaku and Inca cultures came to prominence. To evaluate this impact, analysis of more recent sediment archives from the remote regions of the Bolivian Andes should be a future research priority.

### **5.8) Acknowledgements**

This research was funded by a NERC Open CASE studentship with the Natural History Museum, London (NE/F008082/1) and a National Geographic Committee for Research and Exploration grant (8105-06). NERC radiocarbon facility support (1287.0408 and 1463.0410) facilitated the core chronology. In addition we thank Eric Martinez Costas and Lydia Meneses Lizarazu for assistance in the field, and John Watson for support with the LECO analyses.

## Chapter 6)

### ***On the identification and interpretation of Late Pleistocene and Holocene Chironomidae from the eastern Bolivian Andes***

In this chapter, all subfossil Chironomidae data from both the Lake Challacaba and Laguna Khomer Kotcha Upper study sites are presented and discussed. This section highlights that the published knowledge of Andean chironomid research is in its infancy and shows how this study compliments and builds upon the existing knowledge gap. Descriptions of the chironomid types discovered are provided and discussed in reference to the data obtained from the sediment cores. A list of chironomid types is provided in Table A4.3. This chapter has been submitted for publication separately:

**Williams, J.J, Brooks, S.J and Gosling, W.D.** On the identification and interpretation of Late Pleistocene and Holocene Chironomidae from the eastern Bolivian Andes.

*Journal of Paleolimnology* (Submitted April 20, 2011; Under review 27 April, 2011).

---

#### **6.1) Abstract**

This paper presents the first palaeolimnological record of chironomid remains from the Bolivian Eastern Cordillera. Taxonomic notes are provided for the 10 chironomid taxa (subfamilies: Chironominae, Orthoclaadiinae and Tanypodinae) identified from the lake sediments. This study highlights the role of chironomid analysis as a supporting proxy for the interpretation of Bolivian sedimentary successions when combined with palynological, charcoal and geochemical data. Analysis of the sediments from Lake Challacaba (17°33.257' S, 65°34.024'W; 3400 m asl) and Laguna Khomer Kocha Upper (17°16.514' S, 65°43.945'W; 4153 m asl) reveals new insights into the response of Chironomidae to environmental change over the last 18,000 years in the Tropical Andes biodiversity hotspot. This study shows that chironomid diversity and abundance in the Tropical Andes is sufficient to investigate the response to regional and local environmental changes, highlighting the sensitivity of chironomids to adjustments in net



moisture balance (water level fluctuations and salinity) and anthropogenic impacts (nutrient input).

At Lake Challacaba, the chironomid and geochemical data indicate periodic desiccation and hypersalinity of the basin c. 4,000–3,460 cal yr BP. The increased abundance of disturbance and high nutrient input tolerant *Chironomus* sp. at c. 1,000 cal yr BP suggests a change of human activity; this supports inferences from the pollen and spore records which indicate elevated pastoral agriculture at this time. The chironomid data provide a more complete picture of the extent to which pre-Columbian cultural groups perturbed their environment. The greatest assemblage change in the chironomid record from Laguna Khomer Kocha Upper occurred at c. 6,380 cal yr BP, concomitant with an increase in marsh woodland taxa, wetter conditions and a rising lake level. No response is recorded in the chironomid assemblage to the onset of burning at the start of the Holocene aridity (c. 10 cal yr BP) which is the major transformative agent for the terrestrial vegetation. The comparison with other proxy data suggests that within-lake processes are more important drivers of chironomid assemblages than terrestrial vegetation or fire regime. It is apparent, however, that the full potential of subfossil chironomid analysis will only be realised once more modern autecological data exists.

## **6.2) Introduction**

Owing to the high chitin content, the head capsules of chironomid larvae (Insecta, Diptera, Chironomidae), are well preserved within lake sediments (Epler, 2001; Velle et al., 2010; Walker, 1987; Walker, 2001). They regularly represent the most abundant group of macro invertebrates found in fresh and brackish habitats and have a worldwide distribution, exploiting large ranges in elevation and temperature (Armitage et al., 1995; Ashe et al., 1987; Ferrington, 2008; Pinder, 1986). Within the life cycle, chironomids have four stages (instars) as larvae, with each stage culminating in moulting of an exoskeletal cuticle or head capsule (Walker, 1987; Section 3.4.3; Figure 3.7). The suitability of chironomids for palaeoecological study is not only a product of the good head capsule preservation and abundance, but also due to their sensitivity to changes in environmental conditions. During the adult stage, mobility through wind dispersal enables them to

follow climatic zones and thus track environmental changes (Brooks, 2005; Walker, 2001).

Previous studies of fossil chironomid assemblages has highlighted their potential to act as an indicator for a broad range of environmental changes (see Section 3.4.3 and Table 3.2). These include; anthropogenic land disturbance and pollution (Kansanen, 1985; Woodward and Shulmeister, 2005), volcanic activity (Araneda et al., 2007), hydrology (Hofmann, 1998), lake pH (Brodin and Gransberg, 1993; Johnson et al., 1990), lake trophic status, (Brooks et al., 2001; Gathorne-Hardy et al., 2007), oxygen regime (Quinlan and Smol, 2001), salinity (Chen et al., 2009; Walker et al., 1995), substrate type and input rate (Schakau, 1991; Verschuren et al., 2000) and water and air temperatures (Brooks and Birks, 2001; Lang et al., 2010; Porinchu et al., 2003; Walker et al., 1991).

Despite the proven value of subfossil chironomids in palaeoenvironmental reconstruction, a paucity of research in the Andes of South America remains a serious limitation to any subfossil investigation of this area. The most significant progress in using chironomids for palaeoenvironmental reconstruction has been made in the Patagonia region of Chile and Argentina (reviewed by Verschuren and Eggermont, 2006). Recent ecological and palaeoecological studies of chironomids have highlighted the improvements possible in resolving taxonomic difficulties when a research focus exists (e.g. the work of Donato et al., 2008; Massaferrero et al., 2005; Massaferrero and Brooks, 2002; Massaferrero et al., 2009). However, nowhere else in the Andes is there an equivalent intensity of research effort and the central Andes (Bolivia/Peru) in particular remains deficient in studies. The only international published inventory of the aquatic Diptera from modern lakes in Bolivia/Peru was collected during the 1978 Catherwood Expedition. Thirty-one genera were recorded from within the subfamilies of Chironominae (6 genera), Diamesinae (1), Orthoclaadiinae (19), Podonominae (2), and Tanypodinae (3). More detailed modern ecological investigation of Lake Titicaca, and the smaller, separate lake of Umayo, revealed only the presence of Orthoclaadiinae, (9 species) and Chironominae (6 species) (see Table 6.1) (Roback and Coffman, 1983). Elsewhere in the Bolivian Eastern Cordillera, taxa from stream and lake systems have also been identified (Table 6.1), but the modern ecologically association is largely unknown.

Altiplano Lake Titicaca and Umayo	Basin of Rio Pilcomayo Piedmont east of the Cochabamba Basin	Basin of Rio Beni Northwest of the Cochabamba Basin	Basin of Rio Grande Rio Rocha, Rio Caine and Laguna Alalay
Chironominae <i>Chironomus</i> (2 species) <i>Paratanytarsus</i> , <i>Polypedilum</i> , <i>Rheotanytarsus</i> , <i>Tanytarsus</i> Orthoclaadiinae <i>Cricotopus</i> (5 species), <i>Corynoneura</i> , <i>Paracladius</i> , <i>Pseudosmittia</i> ,	Chironominae <i>Polypedilum</i> , <i>Rheotanytarsus</i> Orthoclaadiinae <i>Cricotopus</i> , <i>Eukiefferiella</i> , <i>Halocladius</i> , <i>Paracricotopus</i> Tanypodinae <i>Ablabesmyia</i> , <i>Paramerina</i>	Chironominae Podonominae Orthoclaadiinae Tanypodinae	Chironominae <i>Chironomus</i> , <i>Dicrotendipes</i> , <i>Polypedilum</i> Orthoclaadiinae <i>Camptocladius</i> , <i>Halocladius</i> Tanypodinae <i>Paramerina</i> , <i>Tanypus</i>
(Roback and Coffman, 1983)	(Oller, 2001)	(Salinas et al., 1999)	(Bervoets et al., 1998; Goitia et al., 2001; Salazar, 2000)

**Table 6.1** Modern chironomid taxa collected from three major hydro-ecoregions of eastern Bolivia (far right 3 columns), and within two lakes situated on the Altiplano (far left column).

This study represents the first investigation into subfossil chironomid remains in the Eastern Cordillera of Bolivia. The eastern slopes of the Tropical Andes are one of the most biologically diverse areas on Earth, with high precipitation caused by the collision of moist, westerly Amazonian air colliding with the Andean mountain chain (Killeen et al., 2007; Myers et al., 2000). Increasing human occupation of the Andes and predicted future climate changes mean the ecology is highly vulnerable (Cincotta et al., 2000; Malcolm et al., 2006). We present the chironomid assemblages from two limnological records from the surrounds of the Cochabamba Basin, extending back 4,000 and 18,000 years. These data provide new insights into the chironomid genera above 3,200 m asl (meters above sea level), and changes in their distribution and abundance during the late Pleistocene and Holocene periods. With reference to previously published palynological, charcoal and geochemical/physical analysis (Williams et al., 2011; Chapter 4; Chapter 5), we explore

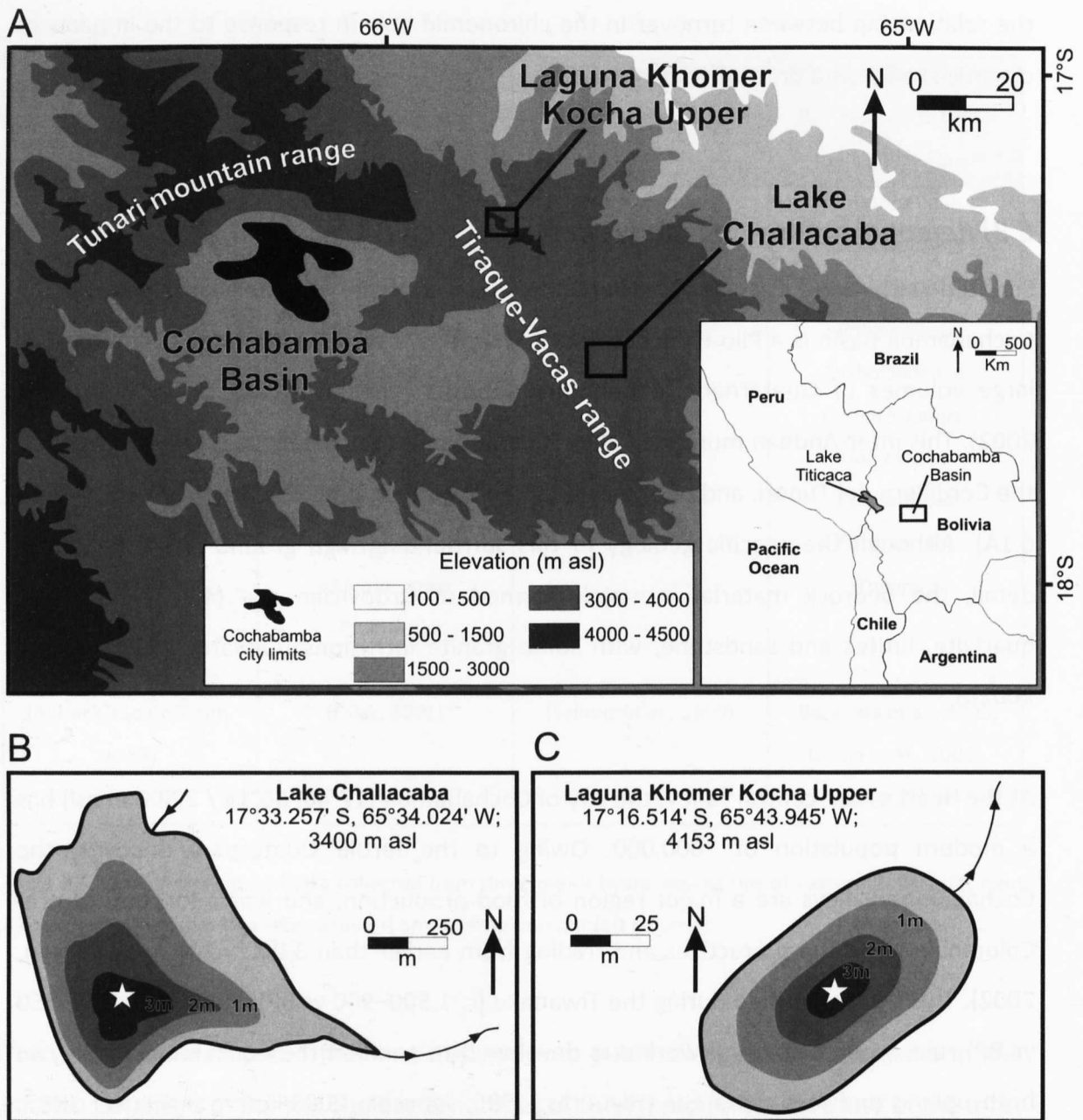
the relationship between turnover in the chironomid taxa in response to the impacts of climatic change and pre-Columbian societies.

### **6.3) Regional setting and study sites**

Situated within the Eastern Cordillera forethrust zone of the Bolivian Orocline, the Cochabamba Basin is a Plio-Pleistocene valley formed after 5.33 Ma and is comprised of large volumes of Quaternary sedimentary deposits (Kennan et al., 1997; McQuarrie, 2002). This inter-Andean montane valley is limited on the northern and western sides by the Cordillera del Tunari, and on the east by the mountain range of Tiraque-Vacas (Figure 6.1A). Although the specific geology of this surrounding high ground is not known in detail, the bedrock material is mainly formed of Ordovician age (488.3–443.7 Ma) quartzite, lutites and sandstone, with some granite intrusions (Cassard, 1999; Kessler, 2002b).

At the heart of the central valley, the city of Cochabamba (17°40', 66°14' / 2,500 m asl) has a modern population of ~600,000. Owing to the fertile Quaternary deposits, the Cochabamba valleys are a major region of food production, and was a location of pre-Columbian agricultural practices and trading from earlier than 3,000 years ago (Hensen, 2002). This was intensified during the Tiwanaku (c. 1,500–900 yr BP) and Inca (c. 650–550 yr BP) rule, when a road network was developed to connect the Cochabamba valley to both upland and lowland areas (Higueras, 1996; Janusek, 2008; Lone and Lone, 1987; Sánchez C., 2008). See Sections 1.4 and 4.2.1 for a full discussion on the ancient road network.

Regional climate, particularly precipitation, is controlled by several systems including; movement of the Intertropical Convergence Zone (ITCZ; Leduc et al., 2009), variability of the South American summer monsoon (SASM; Zhou and Lau, 1998), and inter-annual variation of the El Niño-Southern Oscillation (ENSO; Chiang, 2009; Philander, 1990). Changes in precipitation are considered to be the predominant feature of future climatic changes (Urrutia and Vuille, 2009; Vuille and Werner, 2005).



**Figure 6.1** Maps showing study site location within Bolivia. **A)** Cochabamba Basin with altitudes, current city extent and study locations marked. Modified from Sánchez (2008). Inset map locates Cochabamba Basin within Bolivia. **B)** Lake Challababa (also know as Pilawitu). Bathymetry shown in metres. Coring location marked (★). **C)** Laguna Khomer Kocha Upper. Bathymetry shown in metres. Coring location marked (★).

The topographic and climatic variation place the Cochabamba region at the confluence of four Tropical Andean ecoregions; the Bolivian Yungas, the Bolivian montane dry forests, the central Andean Puna and the central Andean dry Puna (Olson et al., 2001). Locally, several species of endemic birds, mammals, amphibians and plants exist (Navarro et al., 2005; Young, 2007), and the Cochabamba Basin is recognised as an important conservation area for the protection of high elevation *Polylepis* woodlands (Fjeldså and Kessler, 1996). High biodiversity and narrow vertical species ranges in sites of complex topography, means even small variations in temperature and precipitation can result in considerable species turnover. As a result, the fauna and flora of the region is highly sensitive to any change in environmental conditions.

Remnants of a large water body that existed within the Cochabamba Basin, together with smaller lakes created by local glaciation features in the surrounding mountain ranges, provides opportunities to obtain palaeolimnological records. In this study, two lake systems north and east of the main Cochabamba Basin are investigated.

### **6.3.1) Lake Challacaba (Vacas Lake District)**

The Vacas Lake District, situated 60 km east of the city of Cochabamba (Figure 6.1A), is a system of six lakes located within a cold (7.2–11.3°C) and seasonally dry (2.6mm/month June–August, 114mm/month January–March), high elevation (>3,000m asl) valley (Hijmans et al., 2005; Ritter, 2000). Within the district, Lake Challacaba is a small, c. 1.5 km<sup>2</sup>, freshwater system, 2.5 km from the settlement of Vacas (17°33.257' S, 65°34.024' W; 3,400 m asl; Figure 6.1B). Lake Challacaba is fed at its northernmost point by a stream from the surrounding mountains and drained via an outflow at the southeast end (Figure 6.1B). At the time of coring (June, 2007), water depth was 3 m, conductivity 332 µS/cm (microSiemens per cm), pH 9.45 and water turbidity (Secchi depth) was 0.58 m.

The Vacas Lake District is positioned within the biogeographic regions of the northern Puna/semi-humid, and sub-humid/Puna and Punean woodlands of the Tunari (Ibisch et al., 2003; Navarro and Maldonado, 2002). However, today the area is dominated by the cultivation of potatoes and other tubers, and has also been heavily impacted by grazing (Gotkowitz, 2007). Further away from direct agricultural impact, and more typical of the

natural vegetation of the Cordillera of Tiraque–Vacas, are a variety of grassland, shrubland and woodland types (Navarro and Ferreira, 2007).

Today Lake Challacaba is surrounded by actively worked agricultural land, much of which is inundated by water during the wetter months. *Myriophyllum* (Haloragaceae) is the dominant component of the aquatic vegetation in Challacaba, and many of the other Vacas lakes, which is an important food source for cattle during the dry season (Ritter, 2000). Other important aquatic vegetation of the Vacas Lake District includes *Lemna* (Lemnaceae), *Schoenoplectus* (Cyperaceae), *Zannichellia* and *Potamogeton* (Potamogetonaceae) (De la Barra, 2003; Molina et al., 2007).

Historically, the Vacas municipality was significant in regional transportation routes (Sánchez C., 2008). The current road passing through the Vacas lake district was once a principle route linking the main Cochabamba Valley and the archaeological sites of Inca Rakay in the west, to those in the southeast such as Inkallajta and Mizque (Higueras, 1996). Given the importance of camelid pastoralism and caravans for pre-Columbian peoples (Lynch, 1983) and the movement of Tiwanaku traders between the main valley and the Mizque enclave (Janusek, 2008), it seems likely that many groups of people would have had direct contact with the Vacas lakes.

#### *Palaeoecological summary*

In June 2007, a 297 cm long sediment core was extracted from the deepest point in Lake Challacaba. Based on three  $^{14}\text{C}$  accelerator mass spectrometry (AMS) dates of bulk gyttja or macrofossil plant remains, the core represents a continuous record of the last c. 4,000 years (Figure 6.2A). The full sediment structure and chronological data is detailed in Section 4.4 and Williams et al. (2011).

The sensitivity of the site to changes driven by human and climatic factors was detected in a multi-proxy analysis of the lake sediments (Williams et al., 2011; Chapter 4). Fluctuations in drought tolerant vegetation (Amaranthaceae and Caryophyllaceae) and calcium carbonate ( $\text{CaCO}_3$ ) indicate two periods of reduced net moisture (c. 4,000–3,370 and c. 2,190–1,020 cal yr BP) compared to wetter episodes between c. 3,370–2190 and c.

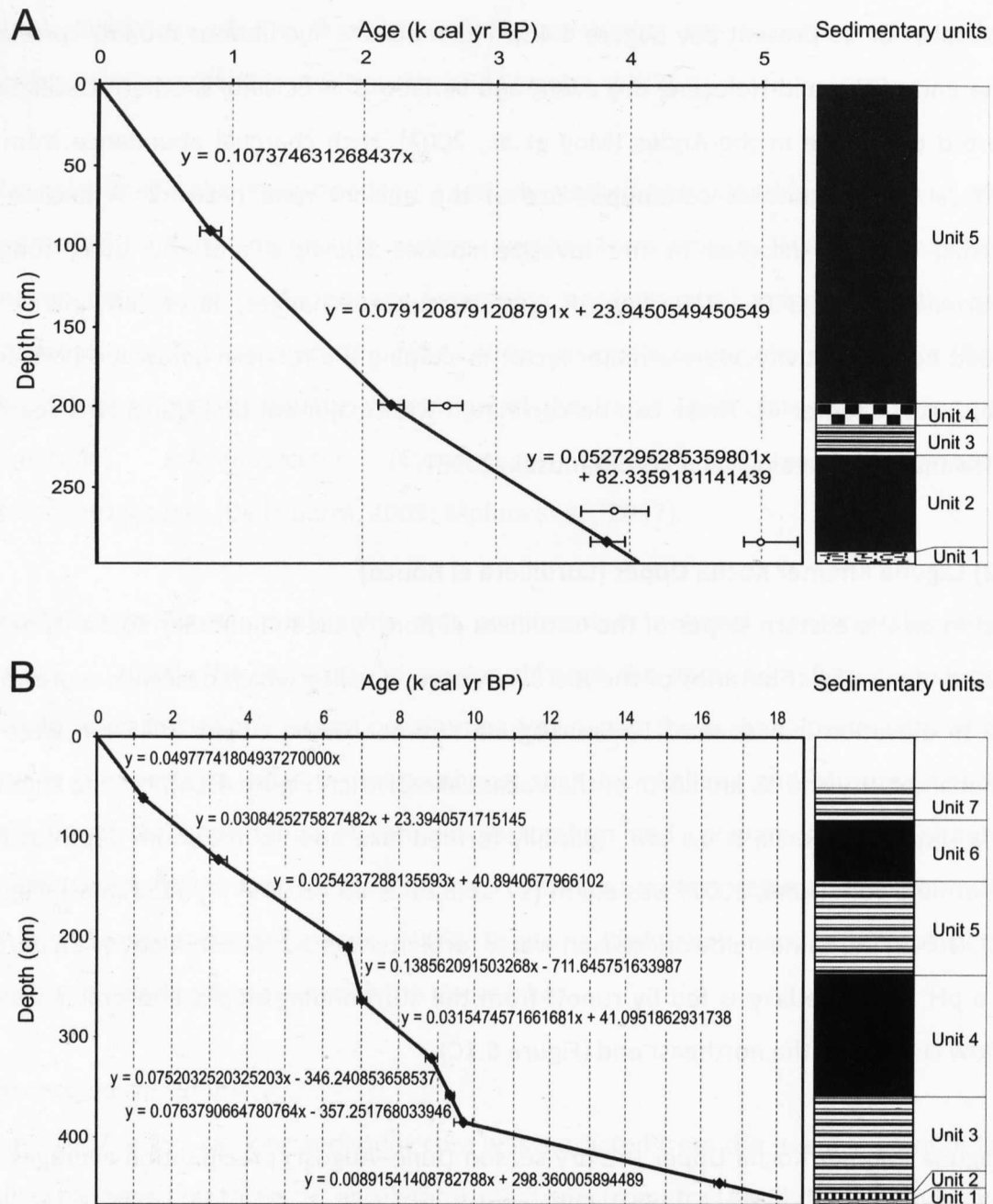


1,020 cal yr BP to present day (Figure 6.4C). The moisture fluctuations broadly correlate to the end of the mid-Holocene dry event and variations in El Niño/Southern Oscillation reported elsewhere in the Andes (Moy et al., 2002). High charcoal abundance from c. 4,000 cal yr BP indicates continuous use of the ancient road network. A decline in charcoal, and an increase in the invasive species *Ludwigia* and the dung fungus *Sporormiella* at c. 1,340–1,210 cal yr BP, suggests cultural changes, particularly increased camelid herding activity, were a major factor in shaping the modern landscape (Williams et al., 2011; Chapter 4). These can be correlated with major cultural transitions seen in the Tiwanaku archaeological record (Janusek, 2008).

### **6.3.2) Laguna Khomer Kocha Upper (Cordillera el Ronco)**

Situated on the eastern slopes of the Cordillera el Ronco, Laguna Khomer Kocha Upper is situated above the tributaries of the Rio San Mateo, a valley which descends more than 2000 m elevation in less than 10 km. Laguna Khomer Kocha Upper is 45 km west of Cochabamba city and 35 km north of the Vacas Lake District (Figure 6.1A). Laguna Khomer Kocha Upper is a small, c. 0.1 km<sup>2</sup>, glacially formed lake and its maximum depth at the time of fieldwork (June, 2007) was 3.6 m (17°16.514' S, 65°43.945' W; 4153 m asl; Figure 6.1C). During the same fieldwork season water turbidity was 3.2 m, conductivity 28 µS/cm and a pH 7.38. The lake is fed by runoff from the surrounding slopes and drains via an outflow channel at the northeast end (Figure 6.1C).

At Laguna Khomer Kocha Upper the dry season (June–August) precipitation averages 13 mm/month this increases to 138 mm/month during the wet season (January–March). Additional humidity is contributed, even during the dry season, by cloud cover which ascends from the valleys to the northwest, depositing large quantities of moisture on the sparsely vegetated slopes (Kessler, 2002b). Mean temperature varies from 4.5 °C for the wet season to 7.6 °C for the dry season (Hijmans et al., 2005) and a local lapse rate is estimated to be ~4.5°C/1000 m (Hertel et al., 2008).



**Figure 6.2** Age-depth curves and sediment stratigraphy of sediment cores. **A)** Lake Challacaba. Sedimentary units: 1) Greenish-grey sandy clay, 2) dark gyttjas with irregular brownish bands, 1-3 cm thick, 3) gyttjas with alternating dark and pale bands, 4) dark mottled gyttjas, and 5) pale to medium-gray gyttjas with progressively higher quantities of clays. **B)** Laguna Khomer Kocha Upper. Sedimentary units: 1) Greenish-gray sandy clay, 2) pale brown coarse sand, 3) dark brown gyttjas with some bands of sandy material, 4) dark brown gyttjas, 5) very dark brown gyttjas, with some strong banding evident, 6) dark brown gyttjas, and 7) very dark brown gyttjas, with some strong banding evident. Sediments upwards of 47 cm were not captured due to their extremely fluid nature. Rejected  $^{14}\text{C}$  dates shown by open circles. Detailed results of  $^{14}\text{C}$  dates previously published (Williams et al., 2011; Sections 4.4 and 5.5; Tables 4.1 and 5.1).

Laguna Khomer Kocha Upper lies in a region of rapid spatial changes in biogeography and vegetation, associated with the steep elevation gradients present in the valley of San Mateo. The lake lies in the sub-humid Puna and transitional Punean woodlands that split the Puna and Yungas zones along the Cochabamba section of the Eastern Cordillera (Ibisch et al., 2003; Navarro and Ferreira, 2007; Navarro and Maldonado, 2002). Today the local landscape immediately surrounding the lake is dominated by Andean tussock forming grassland, within which are pockets of woodland dominated by the tree genus *Polylepis* (Rosaceae). A low (<2 m) glacial moraine separates the lake from an area of flat, waterlogged ground, which is likely to represent an infilled lake of similar size. Today there is minimal sign of human impact at Laguna Khomer Kocha Upper and examination of the *Polylepis* woodland patches surrounding the lake revealed no indications of exploitation.

#### *Palaeoecological summary*

A 413 cm sediment core was extracted from the deepest point of Laguna Khomer Kocha Upper during the 2007 dry season. The chronology for the succession was derived from <sup>14</sup>C AMS dating of three bulk sediment samples and five samples comprised of picked charcoal fragments (Figure 6.2B; Chapter 5), and revealed a sedimentary succession starting at c. 18,100 cal yr BP. The uppermost 47 cm (c. 950 years) of sediment could not be retrieved due to the extremely fluid nature of the material. A full description of the sediment structure and chronological data has already been published (Chapter 5).

The sediment record from Laguna Khomer Kocha Upper shows that fire regime, governed by climatic variation, has long been a transformative agent in eastern Andean ecosystems (Chapter 5). The fossil charcoal record from Laguna Khomer Kocha Upper demonstrates that before c. 14,500 cal yr BP ago fire was virtually absent from the landscape surrounding the lake. The deglacial warming, (c. 18,000–14,500 cal yr BP) coupled with relatively moist conditions free from fire allowed locally growing high Andean *Polylepis* woodland to expand. Between c. 14,500–10,000 cal yr BP burning was minimal but still quickly began to transform the local vegetation as woodland was probably restricted to areas naturally protected from fire. A major increase in burning 10,000–6,400 cal yr BP almost completely removed high Andean woodland from around the lake. The increase in

fire was probably a function of region-wide aridity (Holocene dry event) which also caused lake water levels to fall. A sharp decline in burning at c. 6,400 cal yr BP, with an increase in marsh woodland (*Alnus*) marked the termination of the Holocene dry event and the return to wetter conditions. *Polylepis* woodland expanded from the pockets it was formerly limited to during the height of the aridity and suggests that fire, led by climate, was critical in determining the niche space available for woodland growth.

As well as recording an environmental history of local vegetation dynamics, the long-distance transport of pollen on upslope winds into Laguna Khomer Kocha Upper provides a background signal of vegetation changes in the lower montane forests. Simultaneous adjustments in both Andean and lowland taxa suggests that vegetation dynamics in the two environments can be linked to a common climatic driver. There is no evidence in the proxy record to indicate that human activity before c. 1,000 years ago, the upper extent of the sedimentary succession, had any impact on the local landscape (Chapter 5).

#### **6.4) Material and methods**

Two sediments cores from each site (Challacaba B and C and Khomer Kocha Upper A and B) were recovered using a cam-modified Livingstone piston corer. Staggered, overlapping starting depths below the sediment-water interface ensured that a continuous record was recovered despite potential loss from some tube ends. All sediment cores were recovered in aluminum tubes (50 or 38 mm diameter) and sealed on site. The sediment-water interface was recovered, where possible, using a Perspex surface sample tube, attached to coring rods. The surface sampler was extruded in the field and continuous subsamples of 1 cm thickness bagged. All sediment recovered was transferred to The Open University cold store (4°C). The sediment cores were split and then sediment divided using a fine strand of wire held at tension.

Analysis of the chironomid head capsules was conducted on subsamples of 1 cm<sup>3</sup>. Following the procedure described by Brooks, Langdon and Heiri (2007), see Appendix A2.6, samples were deflocculated in 10% (KOH), heated to 70°C for 5 minutes, sieved and separated into two size fractions (90-212 and >212 µm). Head capsules were picked by

hand from a sorting tray under a binocular microscope (Olympus SZX12) at  $\times 12.5$ – $25\times$  magnification and progressively dehydrated. Depending on size and fragmentation of head capsules, between 1 and 5 were mounted ventral side up under 6 mm diameter coverslips onto a microscope slide. Identification was subsequently achieved using a Nikon Eclipse 50i microscope at  $\times 400\times$  magnification with reference to relevant keys (Brooks et al., 2007; Dieffenbacher-Krall et al., 2008; Epler, 1995; Epler, 2001; Rieradevall and Brooks, 2001 ; Wiederholm, 1983). Stratigraphic diagrams were plotted using the program C2 (Juggins, 2003). The procedures for radiocarbon, palynological, charcoal, geochemical and physical analysis followed standard protocols which have been described in full elsewhere (Williams et al., 2011; Chapter 3; Sections 4.3 and 5.4; Appendix A2).

## **6.5) Results**

### **6.5.1) Taxonomic notes**

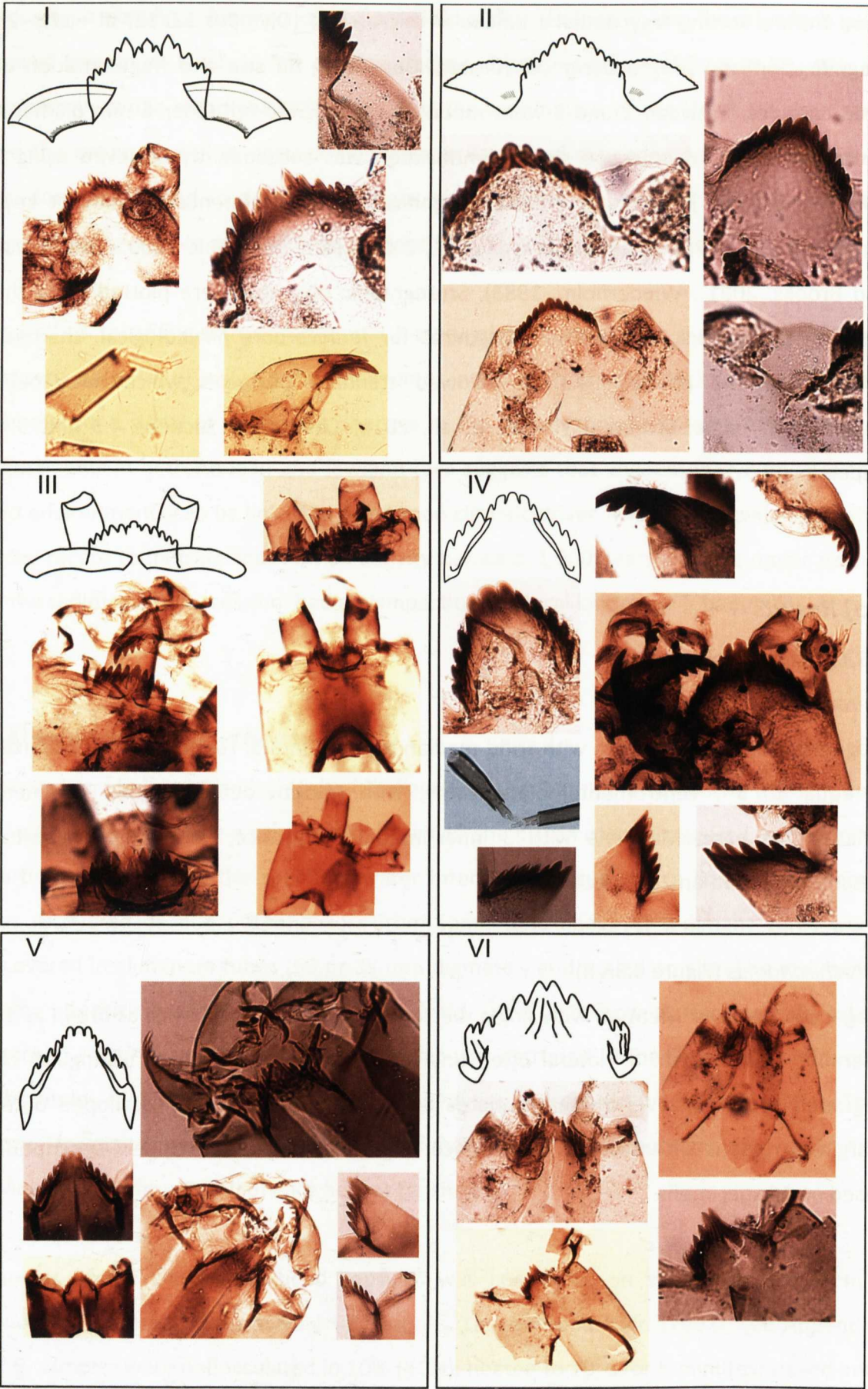
#### *Chironomus* (Figure 6.3A I)

Diagnostic features: Mentum with trifold median tooth. 6 lateral teeth. 4<sup>th</sup> lateral shorter or equal to 5<sup>th</sup>. Ventromental plates large, with smooth outer margin. Prominent striations at base. Mandible with 3 inner teeth. Occurrence: Found in Challacaba. Description based on 216 specimens.

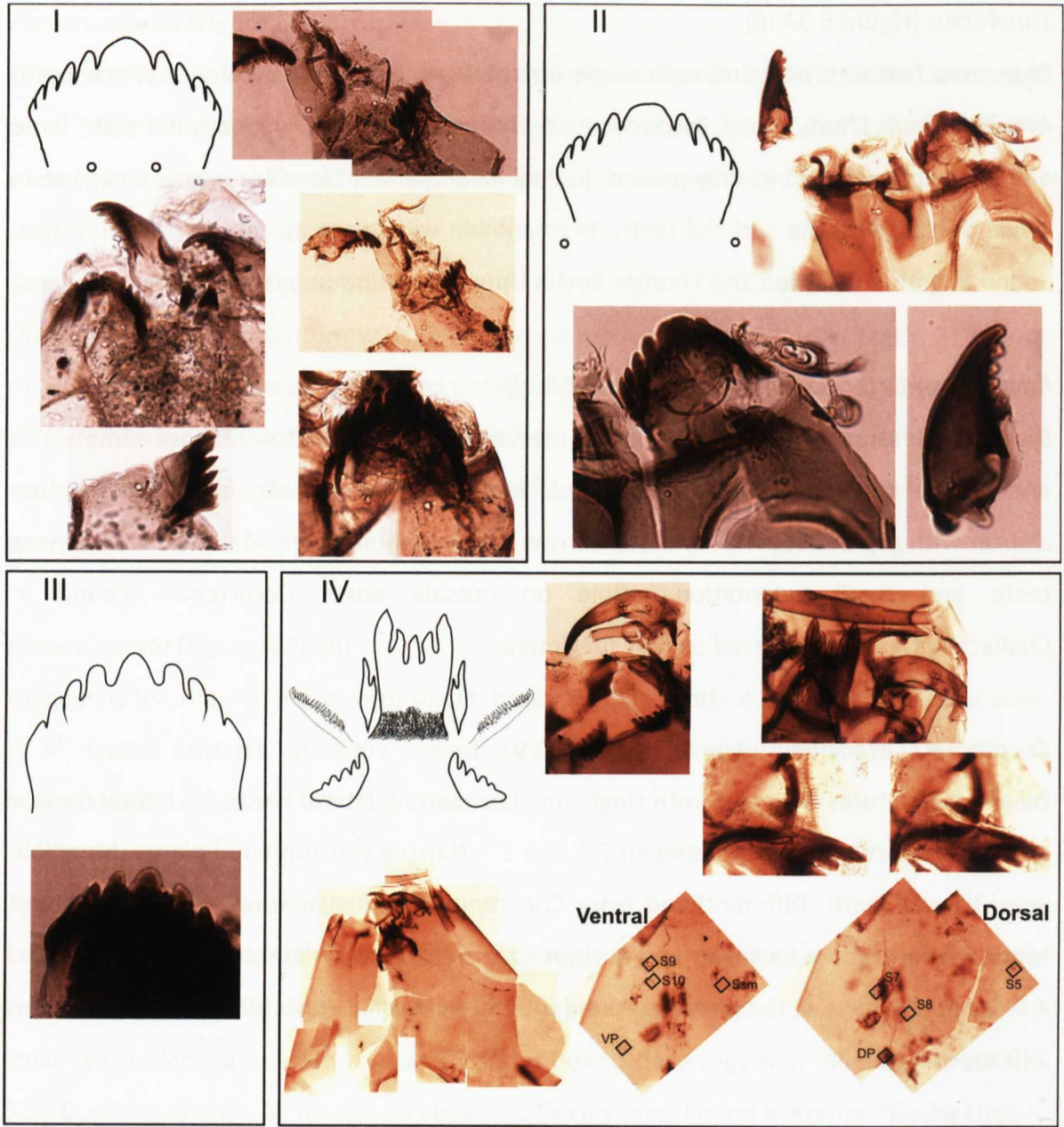
#### *Parachironomus* (Figure 6.3A II)

Diagnostic features: Mentum with single median tooth. Often up to twice as broad as 1<sup>st</sup> lateral. 7 lateral teeth. 7<sup>th</sup> lateral often tiny and sometimes difficult to distinguish on degraded specimens. Ventromental plates large, triangular and with scalloped outer margin. Striations often visible. Occurrence: Found in Challacaba Upper. Description based on 10 specimens.









**Figure 6.3** Line drawings and photographs of key subfossil chironomid head capsules from Lake Challacaba and Laguna Khomer Kotcha Upper. **A; opposite page)** I) *Chironomus*, II) *Parachironomus*, III) *Tanytarsus* IV) *Cricotopus* / *Orthocladius* type I, V) *Cricotopus* / *Orthocladius* type II, VI) *Limnophyes* / *Paralimnophyes*. **B; above)** I) *Paracricotopus*, II) *Smittia* / *Parasmittia*, III) *Pseudosmittia*, IV) *Apsectrotanypus*.



*Tanytarsus* (Figure 6.3A III)

Diagnostic features: Mentum with single notched median tooth. 5 pairs of lateral teeth evenly spaced. Short, broad, blunt spur on antennal pedestal. Post-occipital plate large and darkly pigmented but only present in final instar larvae. Mandible with 3 inner teeth, single dorsal tooth, no surficial teeth. Premandible with three apical teeth. Occurrence: Found in both Challacaba and Khomer Kocha Upper. Description based on 278 specimens.

*Cricotopus / Orthocladius type I* (Figure 6.3A IV)

Diagnostic features: Mentum with single median tooth. Median tooth about same width and of equal or marginally taller height to 1<sup>st</sup> lateral tooth. 6 lateral pairs. 2<sup>nd</sup> lateral often shorter with gap between 2<sup>nd</sup> and 3<sup>rd</sup>. Narrow ventromental plates. Mandible with 3 inner teeth and small indentation visible on outside edge. Occurrence: Found in Challacaba. Description based on 418 specimens.

*Cricotopus / Orthocladius type II* (Figure 6.3A V)

Diagnostic features: Mentum with single median tooth. 6 lateral teeth. 2<sup>nd</sup> lateral narrow and often shorter with gap between 2<sup>nd</sup> and 3<sup>rd</sup>. Narrow ventromental plates. Mandible with 3 inner teeth. Differentiated from *Cricotopus / Orthocladius type I* by 2<sup>nd</sup> lateral tooth width, which is narrower and positioned closer to the 1<sup>st</sup> lateral tooth in *Cricotopus / Orthocladius type II*. Occurrence: Found in Khomer Kocha Upper. Description based on 240 specimens.

*Limnophyes / Paralimnophyes* (Figure 6.3A VI)

Diagnostic features: Mentum with one pair of median teeth, and five lateral teeth. Teeth decrease in size laterally, although the outer two are of similar size. Outer edge of 5<sup>th</sup> lateral distinctly inwardly curved. Banding can often be seen, particularly in the median region. Rounded projections below outer teeth of mentum. No specimens with mandibles or premandibles found. Occurrence: Found in both Challacaba and Khomer Kocha Upper. Description based on 3 specimens.

*Paracricotopus* (Figure 6.3B I)

Diagnostic features: Mentum with single, broad median tooth. 5 lateral teeth. Outer edge of 5<sup>th</sup> lateral distinctly inwardly curved. Setae submenti positioned centrally below mentum. Occurrence: Found in Challacaba. Description based on 8 specimens.

*Smittia* / *Parasmittia* (Figure 6.3B II)

Diagnostic features: Mentum with single, broad median tooth. 5 lateral teeth. 5<sup>th</sup> lateral often tiny and sometimes difficult to distinguish on degraded specimens. Outer edge of 5<sup>th</sup> lateral distinctly inwardly curved. Setae submenti positioned near to base of ventromental plates. Occurrence: Found in Khomer Kocha Upper. Description based on 1 specimen.

*Pseudosmittia* (Figure 6.3B III)

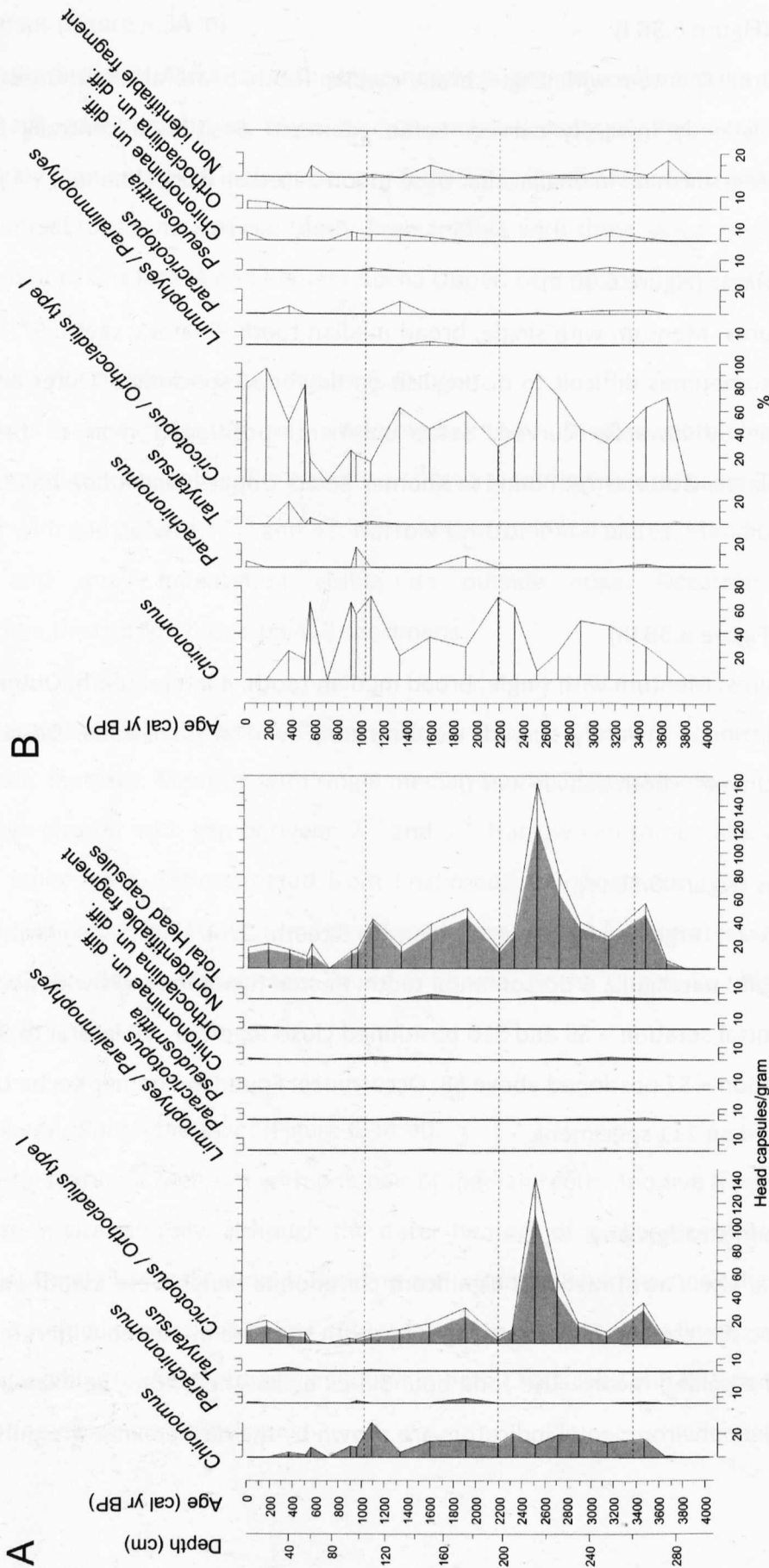
Diagnostic features: Mentum with single, broad median tooth. 4 lateral teeth. Outer edge of 4<sup>th</sup> lateral distinctly inwardly curved. Occurrence: Found in Challacaba. Description based on 2 specimens – both heavily worn.

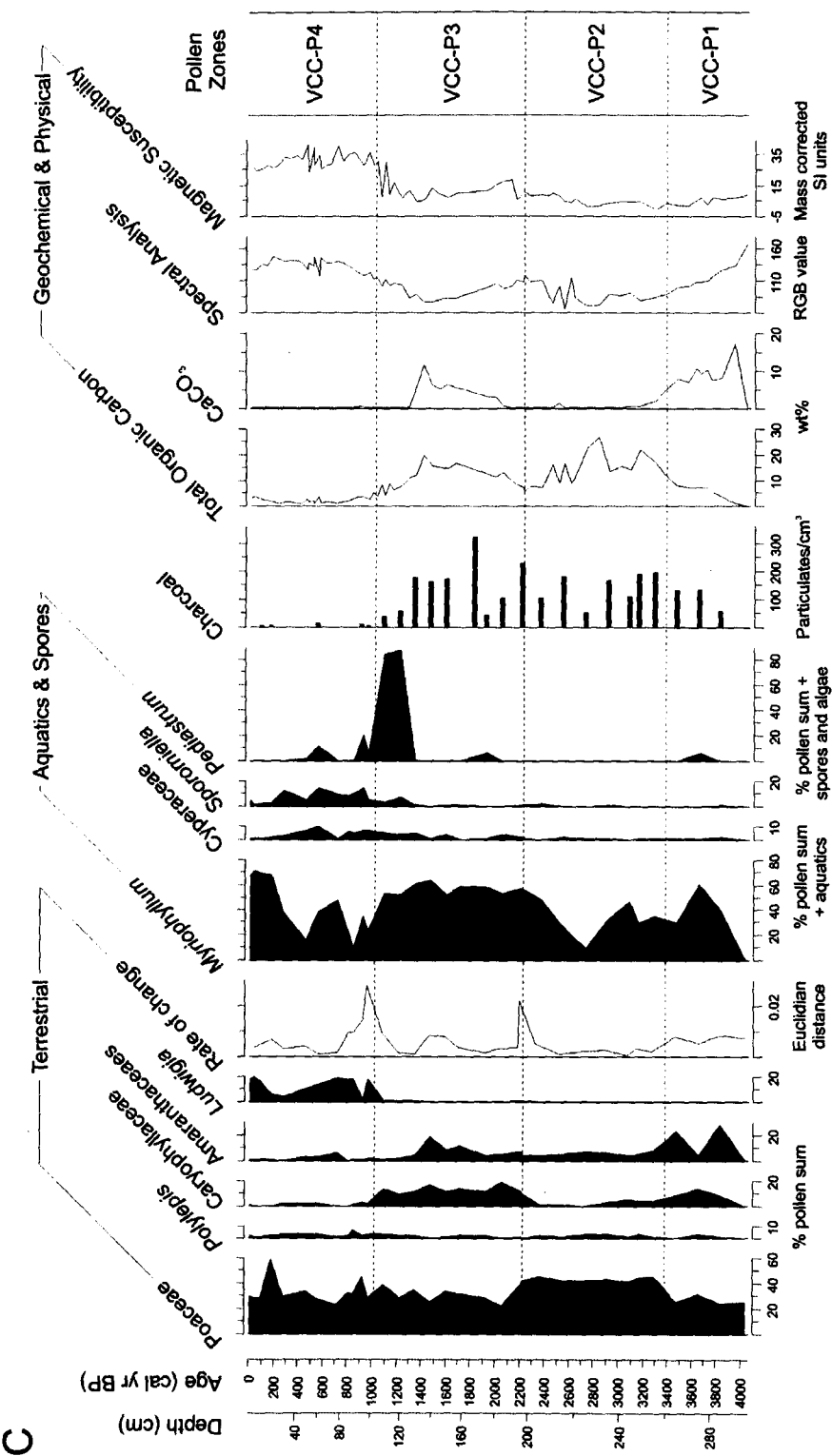
*Apsectrotanypus* (Figure 6.3B IV)

Diagnostic features: Large head capsule. Ligula with 5 teeth. Central tooth shortest, outer teeth longest. Bifid paraligula. 5 dorsomental teeth. Pecten hypopharyngis with about 15 small teeth. Ventral setation – S9 and S10 positioned close together. VP lateral to S9 and S10. Dorsal setation – S7 positioned above S8. Occurrence: Found in Khomer Kocha Upper. Description based on 211 specimens.

### 6.5.2) Chironomid stratigraphy

After zonation analysis no statistically significant chironomid zones were identified from either site and so the chironomid assemblages for both sites are discussed with reference to the rest of the palaeo record. The zone boundaries established from the examination of the other palaeoenvironmental indicators are shown by the dashed lines in Figures 6.4 and 6.5.





**Figure 6.4** Palaeolimnological data for Lake Challacabá. Horizontal lines represent sample points. Dashed horizontal lines indicate the position of Lake Challacabá pollen zones (VCC-P 1-4), established by optimal sum of squares partitioning (Birks and Gordon, 1985) performed using the software ZONE v. 1.2 (Lotter and Juggins, 1991). Assessment of zonal significance was subsequently completed using the broken-stick model (Bennett, 1996; Birks, 1998) in the software BSTICK v. 1.0 (Line and Birks, 1996). **A; opposite page**) Subfossil chironomid concentration data for Lake Challacabá, counting half head capsules as one. Inner grey shaded area marks concentrations when counting half head capsules as half. **B; opposite page**) Subfossil chironomid percentage data Lake Challacabá. **C; above**) Summary pollen, spore, algal, charcoal, and geochemical / physical data Lake Challacabá (Chapter 4; Williams et al., 2011).

### Lake Challacaba

Twenty-two samples were analysed from the c. 4,000 year sedimentary succession of Lake Challacaba, at an average sampling resolution of 200 years (median: 189). Three samples (76, 284 and 295 cm) contained no head capsules (Figure 6.4A and B). Of the remaining samples, the average head capsule concentration per gram (hc/g) was 40, with a maximum of 156 hc/g at 215 cm (c. 2,520 cal yr BP), and minimum of 7 hc/g at 275 cm (c. 3,650 cal yr BP). In total seven chironomid taxa were identified: *Chironomus*, *Parachironomus*, *Cricotopus/Orthocladius type I*, *Limnophyes/Paralimnophyes*, *Paracricotopus*, *Pseudosmittia* and *Tanytarsus* (Figure 6.3A and B).

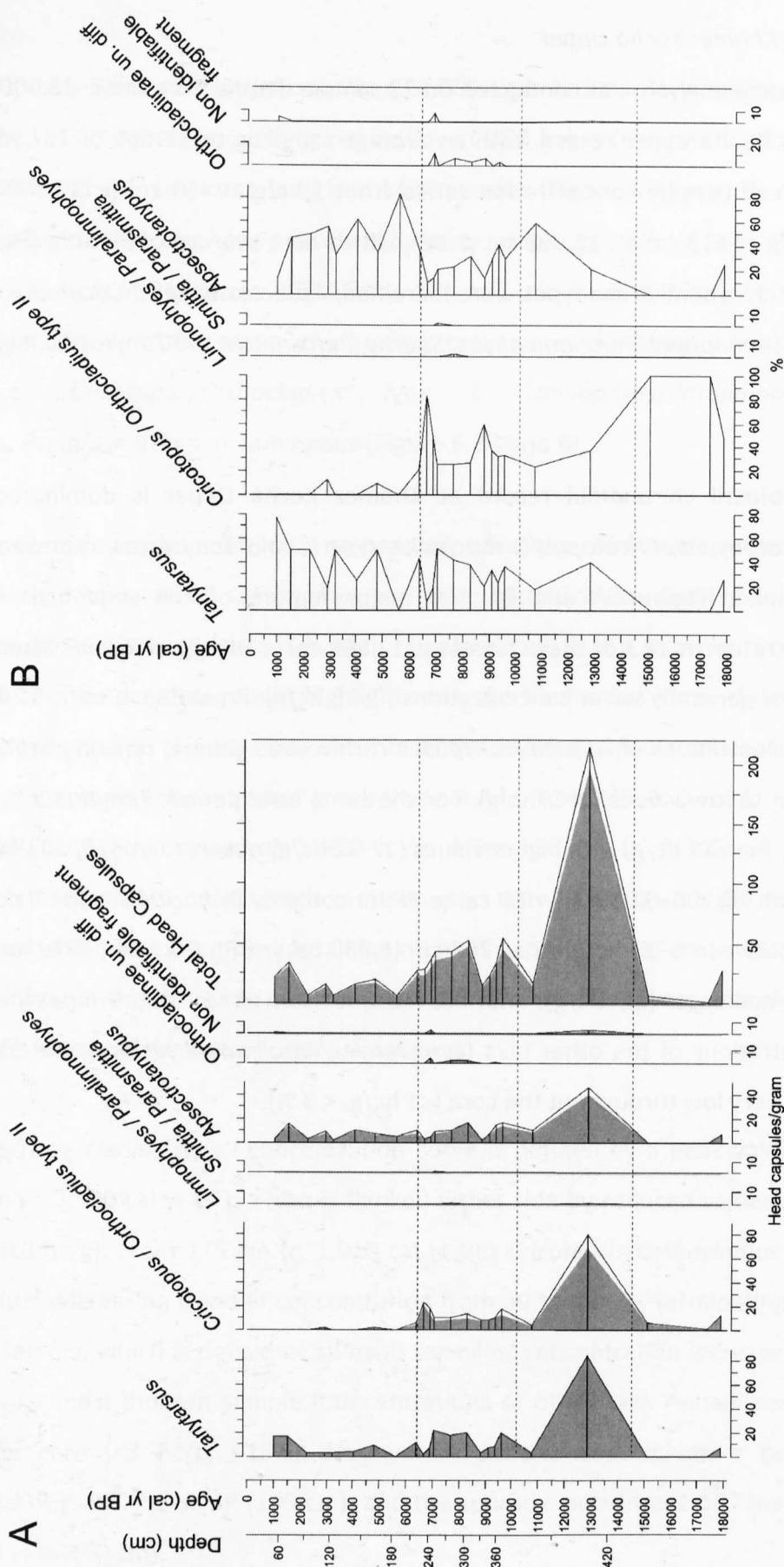
With the exception of samples containing no head capsules, the chironomid record from Lake Challacaba is dominated by *Chironomus* and *Cricotopus/Orthocladius type I*, which together constitute 75-100% of the taxa in each sample (Figure 6.4B). As other taxa were at low abundances, the percentage plot highlights only the fluctuation in the dominance between these two taxa so the data are also presented in head capsule concentrations (Figure 6.4A). *Chironomus* concentration is relatively stable from 265–150 cm (c. 3,460–1,590 cal yr BP) with abundances of 11–20 hc/g. After 130 cm (c. 1,340 cal yr BP) concentration is reduced (<9 hc/g) which is interrupted only by a maxima (30 hc/g) at 110cm (1,090 cal yr BP) and a sample containing no head capsules at 76 cm (c. 710 cal yr BP). At some point between 370 and 190 cal yr BP, *Chironomus* disappears entirely from the record and is absent in the two uppermost samples.

The *Cricotopus/Orthocladius type I* concentration curve is defined by a peak value (142 hc/g) at 215cm (c. 2,520 cal yr BP), which is flanked either side by reduced values at 248 and 197 cm (<10 hc/g). From 175 cm (c. 1,910 cal yr BP) *Cricotopus/Orthocladius type I* displays a gradual decreasing trend in concentration from 30 to 4 hc/g, terminating at 76 cm. After this sample, which is devoid of all head capsules, concentration increases (>15 hc/g) towards the most modern sample. Concentrations of other taxa remain very low throughout the core (<3 hc/g, <18%). Noteworthy occurrences include a peak in *Parachironomus* at c. 960 cal yr BP (100 cm), and the sporadic occurrence of *Tanytarsus* from c. 560 cal yr BP (60 cm).

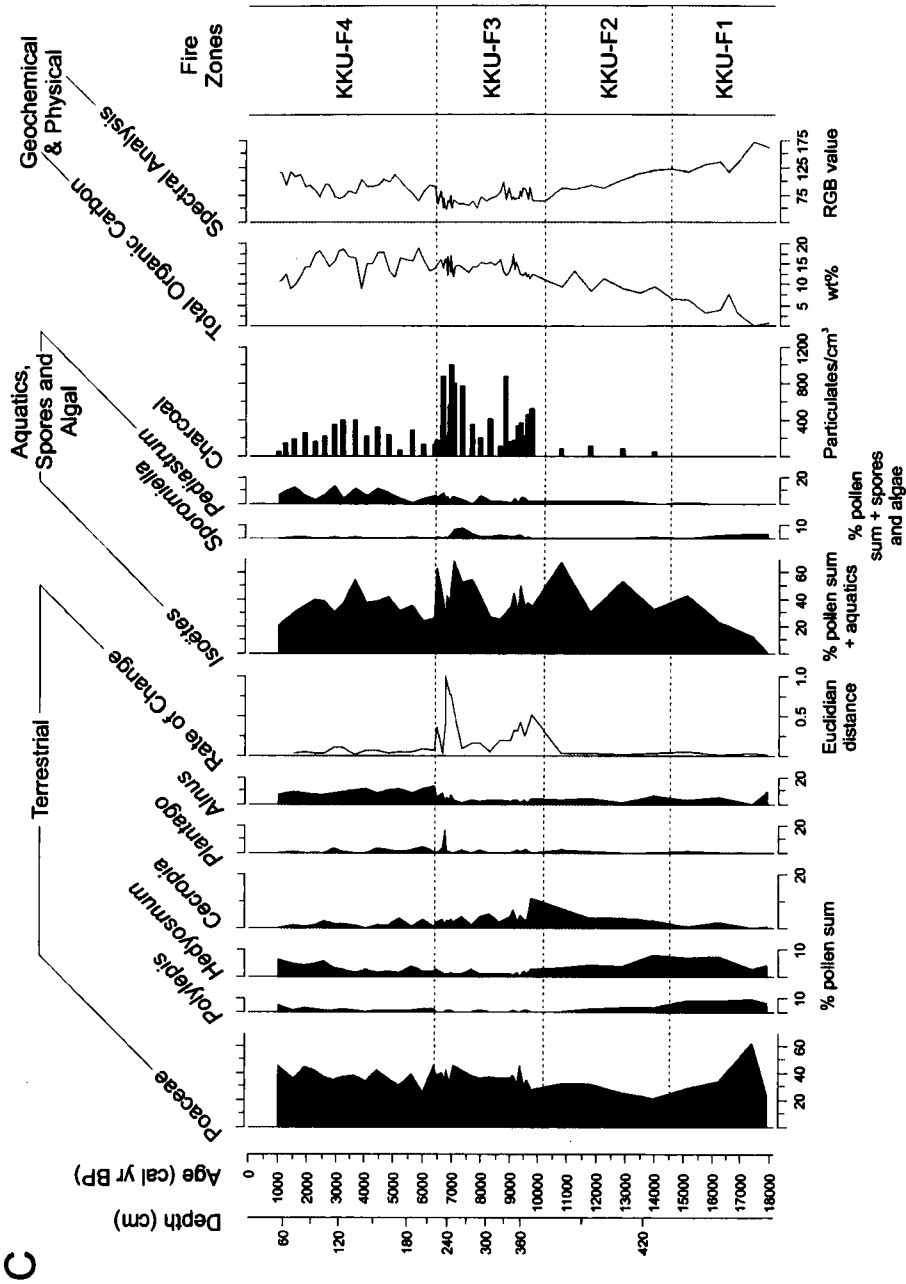
### *Laguna Khomer Kocha Upper*

Chironomid analysis was conducted on 23 sample depths from the c. 18,000 year Laguna Khomer Kocha Upper record, with an average sampling resolution of 767 years (median: 633). Head capsule concentration varied from 1 hc/g at 453 cm (c. 17,350 cal yr BP) to 215 hc/g at 413 cm (c. 12,858 cal yr BP), with a core average of 33 hc/g (Figure 6.5A and B). Five chironomid taxa types were identified; *Apsectrotanypus*, *Cricotopus/Orthocladius type II*, *Limnophyes/Paralimnophyes*, *Smittia/Parasmittia* and *Tanytarsus* (Figure 6.3A and b).

The subfossil chironomid record at Khomer Kocha Upper is dominated by 3 taxa, *Apsectrotanypus*, *Cricotopus/Orthocladius type II*, and *Tanytarsus*, representing >90% in all samples (Figure 5A and B). The major feature of the sequences is a peak in concentration in all 3 of these taxa at c. 12,858 cal yr BP, which occurs after a 5,000 year period of generally lower concentrations (0–25 hc/g). From 396.4Cm (c. 10,700 cal yr BP) the concentrations of *Apsectrotanypus*, a carnivorous genera, remain at relatively stable, medium to low values (2–17hc/g). For the same time period, *Tanytarsus* concentrations are less than 11 hc/g, with higher values (17–20hc/g) observed at 376, 303–263 and 71–51 cm. From 10,700–6,380cal yr BP cal yr BP, *Cricotopus/Orthocladius type II* concentrations range between 5–23 hc/g. After 203 cm (6,380 cal yr BP), *Cricotopus/Orthocladius type II* values decrease (<2 hc/g) and are absent from 6 of the 9 uppermost samples. Concentrations of the other taxa (*Limnophyes/Paralimnophyes* and *Smittia/Parasmittia*) remain very low throughout the core (<1 hc/g, < 3 %).







**Figure 6.5** Palaeolimnological data for Laguna Khomer Kocha Upper. Horizontal lines represent sample points. Dashed horizontal lines indicate Laguna Khomer Kocha Upper fire zones (KKU-F 1-4), determined by visual examination of changes within the charcoal record. **A; opposite page** Subfossil chironomid concentration data for Laguna Khomer Kocha Upper, counting half head capsules as one. Inner grey shaded area marks concentrations when counting half head capsules as half. **B; opposite page** Subfossil chironomid percentage data for Laguna Khomer Kocha Upper. **C; above** Summary pollen, spore, algal, charcoal, and geochemical / physical data for Laguna Khomer Kocha Upper (Chapter5; Williams, 2011).

## 6.6) Discussion

The analysis of the subfossil chironomid assemblages from the sediments of Lake Challacaba and Laguna Khomer Kocha Upper, has, for the first time, revealed their sensitivity to long-term ecosystem changes in the eastern Bolivian Andes. Although low in diversity (5–7 taxa types per site) and average abundance (<40 hc/g), this new inventory of taxa over the last 18,000 years, provides the first step forward in the understanding of Bolivian chironomids. When placed within the framework of change already established from the analysis of the other palaeoenvironmental proxies, adjustments observed in the dominant chironomid taxa offers valuable insight into the impacts of environmental shifts and pre-Columbian cultural change, on freshwater macro invertebrates.

### 6.6.1) Lake Challacaba

The 4,000 year record from Lake Challacaba spans a complicated period of changes in moisture balance and human occupation. These changes resulted in shifts in the abundance of dry tolerant and aquatic plant taxa, as well as nutrient and sediment input (Figure 6.4). Although dominated by only two taxa, the chironomid assemblage from the sediments of Lake Challacaba provide new insights into the response of lake biota to these shifts.

#### *Lake establishment and moisture/lake level fluctuations*

The complete absence of chironomid head capsules in samples prior to c. 3,650 cal yr BP, supports the previous interpretation that the early basal sediments from the site represent a period of lake formation. Pollen preservation and organic sediments indicate that a permanent lake was present at Challacaba from c. 3,820 cal yr BP. However, it was not until c. 200 years later that chironomids are preserved within the lake sediments. In addition, very low concentrations (<7hc/g) of chironomid head capsules before 3,460 cal yr BP also suggest that conditions for chironomids were poor. Chironomids are known to be rapid colonisers of water bodies (Ruse, 2010) so this apparent 400 year period of minimal chironomid abundance in a permanent lake is intriguing. Chironomids are tolerant to a wide of range of salt concentrations (Armitage et al., 1995) and have been shown to be valuable in the reconstruction of changes in past water salinity (e.g. Chen et al., 2009). However, larval numbers have been shown to decline with increasing salinity

(Ólafsson et al., 2000) and African sites have revealed chironomids to be absent from poly- to hypersaline lakes (Verschuren and Eggermont, 2006). Therefore, it is plausible that exceptionally low water levels at Challacaba before c. 3,460 cal yr BP, possibly with periodic desiccation, resulted in a hypersaline lake. This interpretation is supported by high  $\text{CaCO}_3$  precipitates in the sediments (Figure 6.4C), which are known to preferentially precipitate out with heightened salinity (Baker et al., 2001).

A peak in the production of *Cricotopus/Orthocladius type I* (60-140 hc/g) at c. 2,700–2,520 cal yr BP, coincides with the decreased abundance of *Myriophyllum* pollen (Figure 6.4C). *Myriophyllum* is a genus of aquatic macrophyte which forms dense populations in lakes and has been observed to predominate in shallow waters, 0.4-4 m deep, but not in hypersaline conditions (Ritter and Crow, 1998; Ybert, 1992). As lake level increases *Myriophyllum* becomes further removed from the centre of the lake (site of core extraction) and is restricted to the shallows, thus becoming a less dominant component of the pollen record. If the decrease in *Myriophyllum* was in response to increased salinity, it is likely a peak in salt tolerant Amaranthaceae would be observed as has been seen at other sites (Bush et al., 2010). As this does not occur at Challacaba, and there are no other indications of decreased water level and thus increased salinity (e.g.  $\text{CaCO}_3$ ), it seems likely that a deepening of the water level resulted in decreased *Myriophyllum* abundance.

The concomitant decrease in total pollen concentration at c. 2,700–2,520 cal yr BP can also be explained by an increased areal extent and deepening of the lake which may have resulted in dilution of the pollen input. Therefore, the more than doubling of *Cricotopus/Orthocladius type I* concentration, whilst *Chironomus* shows a marginally decreasing trend, appears to be in response to a factor of lake deepening. The observation that the head capsule concentrations of the two dominant chironomid types show different patterns at this point supports an interpretation that this increase in *Cricotopus/Orthocladius type I* production is not an artefact of other lake basin processes such as decreased sedimentation rate, which should cause similar effect on all taxa head capsule numbers. Although a eurytopic organism at genus level (Brooks et al., 2007), lake

deepening and the likely associated drop in salinity and temperature appears to be favourable to *Cricotopus/Orthocladius type I* abundance.

#### *Human impacts*

The first significant occurrence of fungal dung spores (*Sporormiella*) at c. 1,280 cal yr BP, and a marked rise in the abundance of green algal remains (*Pediastrum*) between c. 1,280–1,090 cal yr BP, has been interpreted to indicate trading and pastoralism intensification at Lake Challacaba (Chapter 4; Williams et al 2011). Analysis of the chironomid record provides further evidence for this interpretation, as a peak in abundance of *Chironomus* is seen at c. 1,090 cal yr BP, as it becomes more than 70% of the total chironomid assemblage. Although the temperature tolerance of *Chironomus* appears to vary between hemispheres (warm tolerant north, cold resistant south) and is still unresolved even within South America, the taxon does appear able to survive in highly disturbed systems (Massaferro et al., 2009). Above all, its tolerance to increased lake nutrients (eutrophication) is well documented (e.g. Armitage et al., 1995; Brodersen and Quinlan, 2006; Brooks, 2000; Brooks et al., 2007; Massaferro et al., 2008). At Lake Challacaba the peak in *Chironomus* abundance is therefore likely to be in response to increased nutrient input, caused by the arrival of substantial numbers of domesticated herbivores (camelids) at the lake site, as indicated by the rise in *Sporormiella* spores (Figure 6.4C). A change in lake trophic status is supported by the maxima in *Pediastrum* which has been shown at other sites to represent increased nutrient in-wash (Paduano et al., 2003; Woodward and Shulmeister, 2005).

After the potential desiccation or hypersaline event which leads to the elimination of chironomids at c. 710 cal yr BP, the abundances of both *Chironomus* and *Cricotopus/Orthocladius type I* recover to low values less than <8 and <20 hc/g respectively. The disappearance of *Chironomus* from the record from c. 250 cal yr BP to present is difficult to interpret but could be related to changes recent human practices, or a warming climate.

### 6.6.2) Laguna Khomer Kocha Upper

Although the last c. 1,000 years are not recorded at this site, the sediments from Laguna Khomer Kocha Upper represent an important record of deglaciation and Holocene environments from the wet eastern slopes of the Andes. As found in the pollen assemblage, relative stability existed within the chironomid record for much of the last 18,000 years. However, some change within the abundances of the 3 dominant taxa does provide valuable first insights into the response of high elevation chironomids to climate adjustments, from what is interpreted to be, a site of minimal human disturbance.

The largest and most significant shift in the chironomid record occurs after c. 6,380 cal yr BP when *Cricotopus/Orthocladius type II* becomes almost completely absent. In Patagonia, *Cricotopus* has been interpreted as a warm tolerant taxa (Massaferro et al., 2009), but the disappearance at Laguna Khomer Kocha Upper at 203 cm does not appear to correlate to any temperature changes detected in the other palaeoenvironmental proxies. However, the decline in *Cricotopus/Orthocladius type II* at c. 6,380 cal yr BP does coincide with a major shift in the overall terrestrial pollen taxa, as shown by higher values in the rates of change (ROC) analysis, and is associated with a marked rise in the percentage abundance of *Alnus* (Andean Alder) pollen. *Alnus* is a pioneer taxa, growing regionally in marsh and riparian transitional Puna woodland habitats (Navarro and Maldonado, 2002), and the increase at this time indicates environmental conditions became locally wetter. This interpretation is supported by a sharp decline in burning and suggests an early ending of the Holocene dry event (Chapter 5). Increased net moisture as well as restricting fire and creating an expansion of regional marsh habitat, also appears to have increased water depth at Laguna Khomer Kocha Upper. This is evidenced by a decline in the abundance of the shallow and cool water loving aquatic taxa *Isoëtes*, indicative of water levels <4 m (Bush et al., 2005; Navarro and Maldonado, 2002; Urrego et al., 2011). The decline in *Cricotopus/Orthocladius type II* with increased water depth is in contrast to the findings from Lake Challacaba, where a peak in abundance was observed with lake deepening. Although we cannot rule out the effect of other controlling factors, the opposite responses of these taxa to increased water depth supports our interpretation that the differences observed between the two *Cricotopus/Orthocladius* types are ecologically meaningful.

Intriguingly, the chironomid record from Laguna Khomer Kocha Upper does not show any response to the onset of burning that was such a dominant driver of the terrestrial vegetation at the onset of the Holocene dry event at c. 10 cal yr BP (Figure 6.5). Rates of change analysis reveal this to also be a major period of turnover in local vegetation, as woodland patches are severely reduced in size. Although there is a slight decline in concentrations of all chironomid taxa at this time, this is probably related to the increase in sedimentation rate. The peak in head capsule concentration of all the taxa at c. 12,858 cal yr BP is likely to also be an artefact of sedimentary processes (i.e. decreased sedimentation rate) owing to the sub-equal responses. The lower sampling resolution in this section of the core inhibits further interpretation.

### 6.6.3) Application considerations

The current paucity of modern autecological data inhibits the use of chironomids as an independent proxy for central Andean palaeolimnological investigations. Only with the knowledge established from other proxies (e.g. pollen) can the chironomid data be interpreted in a meaningful way. Although the average abundance of chironomid head capsules per sample in this study was low (<40 hc/g), the low taxon richness allows for important shifts in the abundance of the most significant taxa to be rapidly assessed. The reduction in diversity observed with elevation in this study, although only based on two locations, is in general agreement with observations elsewhere, which show a hump-shaped relationship with taxon richness and elevation, with low richness at the extremes (Bigler et al., 2006; Nyman et al., 2005). As previously discovered (Walker, 1987), this study supports the conclusion that Orthocladiinae head capsules are more prone to splitting than other subfamily groups. However, in this instance, minimal difference in the interpretation, when referring to concentration data, is observed between counting split head capsules as half (0.5) or whole (1). With such low taxon richness, the use of percentage data in representing the changes observed through time should be done so with caution as it can easily result in misinterpretation. For example, in the Laguna Khomer Kocha Upper record, the percentage data of *Apsectrotanypus* shows increased abundance after c. 6,500 cal yr BP, while the concentration data reveals no significant change occurred (Figure 6.5A and B).

## **6.7) Conclusions**

The first investigation of subfossil Chironomidae from the eastern Bolivian Andes reveals their sensitivity to long-term environmental changes over the last 18,000 years, as shown by comparison to other palaeoenvironmental proxies. As a preliminary step in addressing the paucity of current chironomid research in Bolivia and the wider central Andes, our results demonstrate that chironomid communities are represented in the lake sediments of tropical, high Andean lakes above 3,200 m asl. From the analysis of sediments from Lake Challacaba and Laguna Khomer Kocha Upper, 10 chironomid taxa were identified from three subfamily groups.

This study highlights that sufficient diversity, head capsule abundance, and species sensitivity exists at high elevation sites to investigate response to regional and local environmental changes. Although preliminary, this research has revealed the sensitivity of chironomids to changes in net moisture balance, and the associated water level fluctuations and salinity. In addition, it is apparent that at sites with a history of severe human impact, as indicated by other multi-proxy analysis, the changes in chironomid assemblages are also related primarily to adjustments in anthropogenic impacts (e.g. increased nutrient input).

Limited taxon richness at high elevation sites is beneficial to the analyst and, importantly, to consistent identification between study locations. With taxonomic consistency key to the use of chironomids as a palaeoenvironmental proxy, research effort in the currently minimally investigated Tropical Andean ecosystems must be on accurate identification. Although shown in this study to be a crucial supporting proxy for the interpretation of Bolivian sedimentary sequences, the full potential of subfossil chironomid analysis will only be realised once a concerted research focus exists, particularly the establishment of a regional training set.



### **6.8) Acknowledgments**

This research was funded by a NERC Open CASE studentship with the Natural History Museum, London (NE/F008082/1) and a National Geographic Committee for Research and Exploration grant (8105-06). NERC radiocarbon facility support (1287.0408 and 1463.0410) facilitated the core chronology. In addition we thank Eric Martinez Costas and Lydia Meneses Lizarazu for assistance in the field, Dr Angela Self for assistance during chironomid identification training, and the NHM for funding attendance at the 9th Subfossil Chironomid Workshop, Copenhagen.

## ***Chapter 7) Palaeoecology and conservation: a case study from the Eastern Cordillera of Bolivia***

This chapter draws together the palaeoecological data presented in this thesis and assesses the implications for conservation in the Cochabamba Basin, Bolivia. First, the current threats to the ecology of the Tropical Andes are summarised. Secondly, arguments in the literature related to the practicalities of using palaeoenvironmental data as a tool for conservation science are considered. Finally, following a summary of the study location and palaeoecological results, a discussion of long-term, local- to regional-scale environmental vulnerability is presented for the Eastern Cordillera of Bolivia. In this final section, the value of palaeoecological data for informing scientists, landowners and policy makers about ecosystem functions is highlighted. The implications of these data when applied to specific questions and study locations are also considered.

---

### ***7.1) Threats to the ecological value of the Tropical Andes***

#### ***7.1.1) Climate threats***

The Tropical Andes is one of the most biodiverse regions on Earth (Myers et al., 2000) and it is under threat from predicted future climatic changes (Malcolm et al., 2006). By the end of the current century (AD 2100), it is anticipated that the region will have warmed by up to 3.5°C, with increased heating (up to 5°C) in the area of the eastern Andean flanks situated higher than 3500 m above sea level (m asl) (Gosling and Bunting, 2008; IPCC, 2007; Urrutia and Vuille, 2009). Since AD 1975, warming of the Tropical Andes accelerated, reaching values of between 0.3-0.4°C yr<sup>-1</sup> (Vuille and Bradley, 2000). In the only study of upslope plant migration rates in the Tropical Andes (eastern Peru), Feeley et al. (2011) observed rates of plant migration of 2.5–3.5 m yr<sup>-1</sup> vertically during a 4 year period (2003/04–2007/08). These rates of upslope migration are much slower than the rates required (5.5–7.5 m yr<sup>-1</sup> vertical) in order for plant species to track the predicted movements of their respective climatic envelopes.

Whilst future temperature adjustments are predicted to be reasonably uniform, predicted changes in precipitation are much less spatially consistent and uncertain (Urrutia and Vuille, 2009). The traditional view for the Andes is that precipitation variation will follow a pattern of decreased precipitation with increasing latitude (as discussed by Killeen et al. (2007)). However, for the eastern Andean flanks, a more complex pattern of precipitation change can be anticipated because the slopes today have been shown to include spatially complex and separate super-humid, humid and dry regions (Killeen et al., 2007). The modern pattern of precipitation is controlled by a variety of factors at both small- and large-scale, include the orientation of the complex topography (i.e. Andes chain and individual valleys), and wind patterns (e.g. South American low-level jet and microclimatic air movement) (Killeen et al., 2007). As well as the spatially separate super-humid, humid and dry regions, elevation gradients (often in excess of 2000 m in 20 km) allows for large changes in climate conditions over relatively little distance. This moisture and temperature variation over short lateral (horizontal) distances results in ecological sensitivity, with small niche space envelopes.

Previous research has postulated that climate stability is linked to conservation value and highlighted several regions within the eastern Tropical Andes as targets for conservation. These include: i) stable super-humid regions, because of the high species number (diversity) and, ii) stable dry valleys due to the number of endemic species they contain (Killeen et al., 2007). However, in order to ascertain the likelihood of moisture stability persisting in the future and/or assist with detailed climate modelling, evidence of environmental change over multi-millennial time scales in these locations is needed.

### **7.1.2) Human threats**

As well as being under threat from predicated climatic changes (e.g. rapid movement of climatic envelopes), the biodiversity in the tropical Andes is also at risk from expanding human populations (Cincotta et al., 2000). Human-driven threats include increased site access (e.g. road building), landuse change (e.g. agricultural; fires and grazing) and exploration/exploitation of natural resources (e.g. mining, oil, gas) (Jarvis et al., 2010). The continuing expansion of human populations in the Andes is placing increased pressure on limited resources, which means that people, as well as biodiversity, are likely to suffer. For example, in the central Andes, glacial retreat is reducing the long-term

sustainability of water supplies (Barnett et al., 2005; Vergara, 2007) and intensive agricultural landuse has caused severe soil degradation and loss of nutrients (Kessler and Stroosnijder, 2006; Zimmerer, 1993). These types of natural provisions, known as “ecosystem services” (Costanza et al., 1987; Daily, 1997), are increasingly being valued in terms of conservation management and in support of sustainable economic growth, particularly in developing countries (e.g. Ecosystem Services for Poverty Alleviation project; <http://www.nerc.ac.uk/research/programmes/espa>).

The presence of, both current and historical, human populations within a landscape is seen by some as a “threat to conservation” due to their general detrimental environmental impact (Jarvis et al., 2010). Consequently it is likely that areas near to human populations, or with a long history of human occupation, are likely to present a greater challenge to conservation than more remote or pristine environments. In locations where humans already depend directly upon the ecosystems the interaction of the populations with the environment must also be considered in terms of: i) conservation management, and ii) sustainable resources, particularly with regard to food security and water availability. To complicate matters further, human impact in the Andes, like climatic change is, and has been historically, spatially non-uniform (see Dillehay, 2008). Evaluating past human impacts in these ecologically rich regions is crucial for understanding the mechanisms which contributed to the patterns of modern biodiversity distribution (Froyd and Willis, 2008).

In summary, it is clear that the current status of the ecosystems in the Tropical Andes are under threat from both climate change and human activity. Further protection and/or assistance seems likely to be required especially given that the ability of species and communities to shift with changing climatic conditions is so severely restricted today by human influence. The vastness of the Tropical Andes, together with the varied climate and associated fauna and flora (see Sections 1.1.1–1.1.2) presents a significant challenge to conservation organisations, which have limited resources and an aim of maximising return. With conservation management encouraged to focus on long-term protection (Blossey, 1999; Verissimo et al., 2002), both for economic and ecological reasons, indications of how ecosystems might respond to future change are critical. To manage

biodiversity efficiently we must fully understand the processes behind the natural observed patterns, but many of the underlying mechanisms governing these distributions have today been destroyed by humans occupation (Nogues-Bravo et al., 2008). Therefore, the only way in which to obtain quantitative data of how ecosystems may change in the short and long-term future, is to look to the past (e.g. Birks, 1996; Dearing et al., 2006). Palaeoenvironmental data, such as that presented in this thesis (Chapters 4–6), provides a means by which to examine the long-term response of ecosystems through not only naturally varying ecological stress levels (climatic changes), but also through times of changing human cultural development (changing anthropogenic impacts).

## **7.2) Conservation insights from palaeoecology**

Examination of past environmental change, identified from fossil record, has already shown that the climatic characteristics of the Tropical Andes have long been non-uniform and/or asynchronous spatially (see Section 1.1.3 and 1.3). Examples of spatial variability include conflicting evidence related to the nature of last glacial period (wet or dry), the timing of deglaciation, the occurrence of glacial re-advance events (e.g. presence/absence of Younger Dryas cooling) and the scale of regional drought (Holocene dry event) (see Chapters 1, 4 and 5 for a fuller discussion). Responding to these climatic adjustments, fossil pollen records provide the ability to trace past movements in vegetation zones over long time scales (>100s years). Although this examination of dynamic biogeography obtained from palaeoecological records is not as precise as modern ecological survey data, it still provides valuable data of biological responses to past climate changes. As such the information gained regarding an area's natural ecological history (Godwin, 1956; Willis and Birks, 2006) allows researchers to not have to take into account the "shifting baselines syndrome" when attempting to quantify how a system has changed (sensu; Papworth et al., 2009; Pauly, 1995). In addition, fossil pollen records can suggest species likely to act as early indicators of ecological change (Davies and Bunting, 2010), alert scientists to unexpected, non-linear changes that may occur (Bush et al., 2010), and indicate communities which are highly vulnerable or resilient to change (Willis et al., 2010).

In response to the identified threats already acting upon the Tropical Andes, some researchers have been able to use palaeoecological data to suggest how conservation in the Tropical Andes must be adjusted to optimise ecosystem protection. Gosling et al. (2009) suggested that “mimicking” natural vegetation patterns is the best conservation approach. Bush (2002) highlighted how the protection of niche space (physical features) is more critical than the transient species and populations currently occupying them, a concept that has also been supported by recent non-palaeo based researchers (e.g. Marris, 2011; Mosblech et al., 2011). However, whether protecting niche space is successful in the most extreme environments (e.g. very high elevation), when there are few species capable of surviving in the difficult conditions at these sites, has not been fully considered. In this situation there may also be a justification for species-specific conservation.

Many of the insights gained from the analysis of palaeoecological data have already begun to be integrated into current ecological understanding and the development of broad-scale conservation concepts. These are generally applicable over large regional scales, often assessing the vulnerability, risk and value of ecosystems as a whole (e.g. Tropical Andes). However, with such heterogeneity of Andean landscapes, particularly the eastern flanks, the influences of climate and human populations differ greatly over short spatial scales and thus the past and likely future changes also vary. This highlights two key questions: i) how has landscape heterogeneity, and spatial variation in climate and human impacts in the eastern Andes, ultimately determined the relative vulnerability of the biodiversity they contain? And, ii) what are the implications of palaeoecological analysis for our future conservation approach on a local scale, with specific local concerns?

With particular reference to the data gathered in this study (Chapters 4–6), the following discussion will explore how relative threats and the magnitude of impacts in the eastern Andes of Bolivia vary spatially. By focussing on the eastern Andean Cordillera, the discussion aims to demonstrate how the conservation concepts previously identified apply on a local, site-specific scale and how biodiversity, environmental conditions and human occupation are interconnected.

### **7.3) The Cochabamba Basin, Eastern Bolivian Cordillera**

As previously discussed in Section 1.4.1, the Cochabamba Basin is a Plio-Pleistocene inter-Andean valley formed after 5.33 Ma and comprises large volumes of Quaternary sedimentary deposits (Kennan et al., 1997; McQuarrie, 2002). The surrounding mountain ranges in the Eastern Cordillera forethrust zone are comprised of quartzite, lutites and sandstone bedrock material of Ordovician age (488.3–443.7 Ma), with some granite intrusions (Cassard, 1999; Kessler, 2002b). Owing to the fertile Quaternary deposits, the Cochabamba valleys today are a major region of food production, and were a location of pre-Columbian agricultural practices and trading from earlier than 3,000 years ago (Hensen, 2002). This was intensified during the Tiwanaku (c. 1,500–900 yr BP) and Inca (c. 650–550 yr BP) rule, when a road network was developed to connect the Cochabamba valley to both upland and lowland areas (Section 1.4.4, Figure 1.12 and Chapter 4; Higuera, 1996; Janusek, 2008; Lone and Lone, 1987; Sánchez, 2008)

Regional climate, particularly precipitation, is controlled by several systems (see Section 1.1.3) including movement of the Intertropical Convergence Zone (ITCZ; Leduc et al., 2009), variability of the South American summer monsoon (SASM; Zhou and Lau, 1998), and inter-annual variation of the El Niño-Southern Oscillation (ENSO; Chiang, 2009; Philander, 1990). The climatic variation and complex topography place Cochabamba at the confluence of four Tropical Andean ecoregions (see Section 1.1.2); the Bolivian Yungas, the Bolivian montane dry forests, the central Andean Puna and the central Andean dry Puna (Olson et al., 2001). Locally, several species of endemic birds, mammals, amphibians and plants occur (Navarro et al., 2005; Young, 2007).

#### **7.3.1) Local environmental concerns**

Cochabamba has a history of environmental deterioration with increases in deforested and eroded landscapes at the cost of productive agricultural lands and ecologically rich ecosystems (Zimmerman, 1993). The roots of increased soil erosion and land degradation may stem from Inca state rule (c. 650–550 yr BP), who developed the Cochabamba valley into a maize production enclave with 14,000 agricultural workers (Lone and Lone, 1987; Wachtel, 1982; Section 1.4.4). Land grabbing following Bolivia's independence (AD 1825) further intensified cultivation and livestock production and depleted the soils of nutrients



rapidly. Water supply problems have also impacted upon the local environment. Driven by adverse economic conditions, increased rural–urban migration caused Cochabamba’s population to grow rapidly, particularly during AD 1980’s. This influx led to increasing water shortages and as a result forced many of the inhabitants to illegally clear and claim lands on the favourable, moist, Tunari foothills, north of Cochabamba city, which are part of Tunari National Park (Sharifi et al., 2002).

Today, detrimental impacts continue upon the landscapes that Cochabamba’s residents rely upon heavily for resource sustainment. These adverse effects on the ecosystem services display a worrying trend and recurring nature. Perhaps the most famous example, common across most developing countries in both lowland and upland area is that of landscape clearance (e.g. forest clearance) and intensive use (e.g. grazing), which results in soil degradation and ultimately land abandonment as productivity declines (for discussion see Barbier, 1997). Across Bolivia, people are becoming increasingly aware of how environmental degradation and ecosystem loss is associated with adverse impacts upon population health. Indeed, in recent months environmental protection in Bolivia has reached worldwide attention following the establishment of 11 new rights for nature, which gives “Pachamama” (Mother Earth) equal rights as humans (Vidal, 2011). This new policy is a direct attempt to stem landscape damage, protect key ecosystems and prevent further escalation of the concerns of many rural populations. For the Cochabamba Basin, one of the corner-stone ecosystems fundamental to rural communities is high elevation woodlands.

### *The Polylepis woodlands*

The arborescent genus *Polylepis* is considered fundamental to the biodiversity of the high Andes (Section 1.1.2). *Polylepis* woodland is one of South America’s most endangered ecosystems, with 15 species of *Polylepis* classified as vulnerable by the International Union for Conservation of Nature (IUCN) (Jameson and Ramsay, 2007; Navarro *et al.*, 2005). Endemic to South America, with a centre of diversity and endemism from central Peru to southern Bolivia (see Chapter 1), *Polylepis* woodlands today are present at more than 5000 m asl (Kessler, 2002a; Navarro et al., 2005). This high altitude survival has been

facilitated by several adaptations including increased frost resistance (Graf, 1981) and protection from increased UV-radiation (González et al., 2007).

*Polylepis* woodlands are fundamental in supporting endemic and habitat specialist species in an otherwise sparse, grassland dominated, landscape (e.g. Cahill and Matthysen, 2007; Young, 2007). As well as the biodiversity *Polylepis* supports, the woodland's social and economic importance marks them as a unique habitat. Used for firewood, construction materials (Macek *et al.*, 2009) and cattle fodder (Fjeldså and Kessler, 1996), the *Polylepis* woodlands have also had symbolic and social significance since Inca (c. 650–550 yr BP) times (Capriles and Bedregal, 2002). Additional ecosystem services provided by *Polylepis* have also been recognised, including the potential role of the woodlands as a substantial carbon sink and future offset, in water regulation and clean water provision, and in soil protection and erosion limitation (see Section 1.1.2; Aucca and Ramsay, 2005; Fehse et al., 2002; Fjeldså and Kessler, 1996; Renison et al., 2010; Teich et al., 2005).

In 1996, the Cochabamba Basin was indicated as a top priority conservation area for protection of *Polylepis* woodland because of the endemism, and the serious problems of increasing soil erosion and water shortages associated with forest removal (Fjeldså and Kessler, 1996). Long-term management and conservation that secures the future of *Polylepis* woodland in the Cochabamba region is especially important as much of the unique flora and fauna is associated with the long-term presence of the woodlands (Fjeldså and Kessler, 1996), and that the pressures applied to the ecosystem are set to intensify as populations and resource demands increase in the future. However, as previously ascertained (Sections 7.1.2 and 7.2), to develop an effective conservation policy, a robust understanding of the region's natural history through periods of varying stress levels is required (Godwin, 1956; Willis *et al.*, 2010; Willis and Birks, 2006). These baseline data provides management targets and indicates how ecosystems are likely to respond to future perturbation.

### 7.3.2) Local palaeoecological records

In order to investigate further the questions raised and to determine the best way to facilitate the integration of palaeoecological data into local conservation issues, two locations from the eastern Bolivian Andes will be primarily used to illustrate this discussion: Lake Challacaba (LC; see Chapters 2 and 4) and Laguna Khomer Kocha Upper (LKKU; see Chapters 2 and 5). Although situated less than 35 km apart in the surroundings of the Cochabamba Basin, examination of the environmental histories at each site reveals how the current and historical circumstance of the two locations is strikingly different, both in terms of climate and human impact. As a result, the vegetation and biodiversity of each location is unique.

#### *Laguna Khomer Kocha Upper*

Laguna Khomer Kocha Upper (LKKU; 17°16.514' S, 65°43.945' W; 4153 m asl;) is situated on the eastern Andean slopes above the super-humid region of the Chapare Yungas forests (Chapter 2). Although 3500 m higher than the most humid area as identified by Killen et al (2007), the LKKU region receives year round moisture input from ground-level cloudcover which ascends on upslope winds from lower elevations, depositing large quantities of moisture on the sparsely vegetated slopes (Section 5.3; Figure 5.2; Kessler, 2002b). This additional moisture input makes the area unique compared to other eastern Andean sites. Today the local area is dominated by Andean tussock-forming grassland, within which are pockets of *Polylepis* woodland. The c. 18,000 cal yr BP sediment record from LKKU, examined in this thesis, shows that fire regime, governed by climatic variation, has long been a transformative agent in eastern Andean ecosystems (see Chapter 5). A major increase in burning (10,000–6,400 cal yr BP) was probably a function of region-wide aridity (Holocene dry event; HDE), which caused lake water levels to fall and severely reduced the abundance of *Polylepis* woodland. At c. 6,400 cal yr BP an increase in marsh woodland (*Alnus*) marked the termination of the HDE and the return to wetter conditions, which allowed *Polylepis* woodland to expand from the pockets to which it was formerly limited during the height of the aridity. Long-distance transport of pollen on upslope winds into LKKU provides a background signal of vegetation changes in the lower montane forests, and shows that adjustments in both Andean and lowland taxa can be linked to a common climatic driver (Chapter 5). In contrast to many other

reconstructed palaeoenvironmental records, there is no evidence of past human influence detected from the sediments of LKKU.

### *Lake Challacaba*

Thirty-five km to the south of LKKU, and within the Vacas Lake District, a 4,000 cal yr BP sediment record from Lake Challacaba (LC; 17°33.257' S, 65°34.024' W; 3400 m asl) has also been investigated in this thesis (Chapter 4; Williams et al., 2011). Situated within a cold (7.2–11.3°C) and seasonally dry (2.6mm/month June–August, 114mm/month January–March), inter-Andean valley (Hijmans et al., 2005; Ritter, 2000), LC is located within a landscape that is today heavily altered by cultivation and grazing (Chapter 2; Gotkowitz, 2007). Historically, the Vacas municipality was significant in regional transportation routes (Sánchez C., 2008). The importance of camelid pastoralism and caravans for pre-Columbian peoples (Lynch, 1983) and the movement of Tiwanaku traders between population enclaves (Janusek, 2008), led many groups of people to have direct contact with the Vacas lakes.

The continuous record of the last c. 4,000 years reveals sensitivity of the site to changes driven by human and climatic factors (Chapter 4; Williams et al., 2011). Fluctuations in drought tolerant pollen taxa (Amaranthaceae and Caryophyllaceae) and calcium carbonate (CaCO<sub>3</sub>) indicate two periods of reduced net moisture (c. 4,000–3,370 and c. 2,190–1,020 cal yr BP) compared to wetter episodes (c. 3,370–2190 and c. 1,020 cal yr BP-present). A decline in charcoal, and an increase in the invasive species *Ludwigia* and the dung fungus *Sporormiella* at c. 1,340–1,210 cal yr BP, suggests cultural changes, particularly increased camelid herding activity, were a major factor in shaping the modern landscape (Chapter 4; Williams et al., 2011). These can be correlated with major cultural transitions seen in the Tiwanaku archaeological record (Janusek, 2008).

## **7.4) Vulnerabilities**

In the following section, a discussion of long-term, local to regional-scale vulnerability is provided, focusing on the Laguna Khomer Kotcha Upper and Lake Challacaba study sites. Although the definition of vulnerability is variable (Adger, 2006), it is here discussed in the context of three main parameters; i) the ecosystem's exposure to stress, ii) its sensitivity (susceptibility to stress), and iii) its resilience (ability to cope with stress).

### **7.4.1) Exposure**

All ecosystems are exposed to some globally-impacting changes (e.g. CO<sub>2</sub> increase and global warming). However, geographical differences (spatial variation) between sites govern the exposure of individual sites to other local stresses. In the eastern Bolivian Tropical Andes, this is primarily the differences in the relative influence of human impact and climatic fluctuation, which can vary even over short distances (see Section 7.1). Although the level and spatial variation in short-term (<50 years) stresses can be assessed through observation and examination of historical records, in order to fully understand the long-term (>50 year) impact on the local ecosystems, a knowledge of past pressures is required. This is especially important considering that biogeography of Andean biodiversity is believed to be a result of long-term impacts of climatic conditions and human intervention. The palaeoecological records from LKKU and LC testify to this spatial variation in climatic and human impacts and help to show the formation of the current ecosystem.

#### *Long-term climate stresses*

The palaeoecological evidence suggests that LKKU, which is situated close to a super-humid climate region, has, when compared to inter-Andean locations such as LC, been in general impacted less by past climate change events. Although a direct comparison can only be achieved over the period c. 4,000-1,000 cal yr BP, the data suggest that the vegetation around LKKU (Chapter 5) shows minimal response to the millennial-scale moisture fluctuations seen at LC (Chapter 4), as indicated by large-scale variation in Amaranthaceae, Caryophyllaceae and CaCO<sub>3</sub>. Additionally, preservation of a water body at LKKU during regional-scale aridity of the mid-Holocene contrasts to the desiccation of LC before 4,000 cal yr BP. So while regional-scale (Andes and Amazon) drought events

occurred, a continuation of ground-level cloud cover at LKKU throughout this time was sufficient to contribute moisture and reduce UV exposure (evaporation), maintaining an inundated lake basin (Chapter 5). The presence or absence of this additional moisture source is directly a result of geographic and topographic location of the site. If super-humid regions are more stable due to geographic setting, as suggested by the palaeo-record of LKKU, they may be consequently less vulnerable to predicted climate changes of the future, particularly precipitation adjustments.

### *Human stresses*

The records from LLKU and LC highlight how the impacts of humans are spatially variable over relatively short distances (<50 km) and are dependent on favourable environmental conditions and resource availability. Areas considered rich in biodiversity might not be under as much threat from human occupation as sites considered ecologically poor today. Moist, high elevation slopes favourable for the development of important ecosystems such as the upper Yungas, are avoided by humans due to the extremes in temperatures, heavy precipitation, difficult access and scarcity of cultivatable lands (see Bush, 2002). While the exposure to human stresses is undoubtedly the reason for the differences seen in degradation at each site, it should not be assumed that all human exposure is necessarily detrimental. Humans were probably present in the landscape around LC for the last 4,000 years (Chapter 4; Williams et al., 2011), but it is only during the last 1,000 years that major impacts of their presence can be seen.

Unless all *Polylepis* woodland clearance was completed in the Vacas Lake District prior to c. 4,000 cal yr BP, the pollen record of LC reveals no systematic or abrupt decline in woodland abundance during this time (Chapter 4; Williams et al., 2011). Although it is clear that modern human impacts are responsible for current clearance and slowing regeneration / re-establishment, predominantly via fire (Hensen, 2002; Renison *et al.*, 2006) and increased grazing impact (Cierjacks et al., 2008; Renison et al. 2004; 2005; Teich et al., 2005), controversy still remains regarding the natural extent of *Polylepis* woodland (Section 1.1.2; Aucca and Ramsay, 2005; Kessler, 2002a). This has big consequences for the understanding of woodland dynamics and the setting of conservation targets. Fjeldså and Kessler (1996) estimated that only 10% of the original

extent remains in Bolivia today, a largely speculative assessment based upon niche-space defined models and the knowledge of a long human history in the Andes (see Section 1.1.2). However, interpolating the current level of human impact upon *Polylepis* forests close to inhabited areas back through history is unwise. To assume the level of detrimental impacts (exposure) that have been observed over recent times (i.e. last 50 years) also occurred since human occupation began, and civilizations formed (e.g. Tiwanaku – last 1000 years), may give misleading interpretation of the previous woodland abundance and structure. Using short-term observations to form views on long-term trends in woodland abundance is naïve and resembles the problems associated with the shifting baseline problems as previously discussed (Section 7.1). Palaeoecological analysis is the only way to resolve this problem and provide data on trends. Using this approach, the LC pollen evidence reveals that there was no significant change in woodland abundance during a time when humans were continually present upon the landscape (Chapter 4; Williams et al., 2011).

In heavily impacted “cultural landscapes” such as the Vacas Lake District, human occupation in the past has certainly been important in shaping the modern ecosystems. However, populations may well have also assisted with the preservation of ecosystems we are striving to conserve (see Froyd and Willis, 2008). For example, *Polylepis* woodlands were strictly protected during Inca (c. 650–550 yr BP) times who had high regard for the naturalness of the woodlands and their symbolic and social meaning, which resulted in very specific forest management (Capriles and Bedregal, 2002). Some of these beliefs are likely to have been perpetuated in modern rural cultures and some practices do exist in modern communities that protect local forest patches as valuable resources (Fjeldså, 2007). If this type of forest stewardship can be developed and expanded, the exclusion of humans from woodland patches would be unnecessary and, perhaps, detrimental to biodiversity conservation. The passing of the new rights for nature laws (Section 7.3.1), inspired by the indigenous Andean spiritual view (Vidal, 2011), may represent a significant step in reintroducing this type forest stewardship.



#### 7.4.2) Sensitivity

The susceptibility and sensitivity of an ecosystem to the stresses imposed upon it are complex. Regionally, *Polylepis* has been shown to be highly sensitive to fire (Gosling et al., 2009), and data from LKKU has shown that when fire increases *Polylepis* woodland is rapidly reduced in abundance (Chapter 5; Figure 5.4). However, while this relationship appears straight-forward, ecosystem responses are complicated by feedback mechanisms which can introduce non-linear changes (see Bush et al., 2010). Palaeoecological data which records species and community-level sensitivity to change is a potentially useful tool in assessing these ecosystem responses.

#### *Ecological indicators*

Mountainous regions have already been identified as sensitive to changes in environmental processes and climate change, so much so that they have been labelled as “early warning indicators” (Ørbæk et al., 2004; Tiberti et al., 2010). However, the changes to expect following future warming are unknown and are certain to be site specific. If sensitive ecological indicators of past environmental change can be identified from the palaeoecological records, they have the potential to be useful markers of future ecosystem shifts.

From the analysis of the Cochabamba records some ecological indicators of change can be suggested. *Hedyosmum*, a genus of tree and shrubs occurring in the Bolivian montane forests below LKKU, shows rapid expansion upslope as climate warms during the deglaciation period (Chapter 5). Modern analysis of upslope migration rates from the eastern Peruvian Andes showed that *Hedyosmum* had one of the fastest (16-25 m yr<sup>-1</sup> vertical) during a four year period when temperatures were warming at around 0.04°C yr<sup>-1</sup> (Feeley et al., 2011). As one of the few taxa potentially able to keep pace with climate changes, *Hedyosmum* is therefore likely to persist and perhaps is less vulnerable to future extinction.

At LC, in a landscape dominated by human occupation, the palaeoecological record shows that the arrival of an invasive plant (*Ludwigia*), associated with human occupation, had the most influence of the lake margin vegetation over the last 4,000 years (Chapter 4;

Williams et al., 2011). With increasing human impact predicted in the region, it seems logical to suggest that additional arrivals could feature in the future, as humans alter the ecosystems, create new niche spaces and act as a transport mechanism (either accidental or deliberate). If, as with the case at LC, species currently present can be shown to have arrived in response to human impacts, it highlights the usefulness of palaeoecology as a tool for addressing many questions regarding biological invasions (Froyd and Willis, 2008). This includes examining the impacts, rates of spread and how we classify species (e.g. how long does a species need to have been present to be classified as a natural ecosystem component?).

### 7.4.3) Resilience

The ability of an ecosystem to cope with stress and absorb disturbance (Holling, 1973), is another topic for which where palaeoecology offers great potential to provide data useful for conservation practice (Froyd and Willis, 2008). Understanding the limits of species/community resilience identifies key ecological thresholds of ecosystem change. Without palaeoecological analysis the critical point of change would remain unidentifiable and unexpected. From the Cochabamba palaeo-records several examples can be cited. Two examples will be discussed, one from changes seen in the terrestrial vegetation, and one in the chironomid assemblage.

#### *High Andean woodland resilience*

*Polylepis* has already been shown to be regionally and locally highly sensitive to fire (see Section 7.4.2), with a rapid reduction at LKKU during the Holocene dry event (HDE) which elevated burning. Despite the decline of *Polylepis* pollen in the record during the HDE (10,100–6,400 cal yr BP) (to less than <1%), woodlands remained present in the locality (probably on the scree slopes, which act as natural fire breaks). The local persistence through the HDE would have helped the re-establishment of larger woodlands once the climate had changed to more favourable wetter and consequently less frequently burnt landscape at 6,400 cal yr BP (see Chapter 5). Although reduced in abundance during the HDE the ability of *Polylepis* to endure unfavourable conditions and not become locally extinct is evidence of its natural resilience to arid climate condition. Small groups of trees preserved in niches governed by micro-climates allowed *Polylepis* to quickly re-establish

at the onset of more favourable conditions. The rapid expansion of *Polylepis* has also been observed periodically in the 370 ka cal BP pollen record from Lake Titicaca, which indicates maximum abundance during transitional warm and wet periods (Gosling et al., 2009; Hanselman et al., 2011).

Although *Polylepis* returned to LKKU after the HDE, the pollen record from Lake Refugio in the eastern Peruvian Andes revealed that woodlands did not re-establish there. The failure of *Polylepis* woodland to re-establish at Refugio has been associated with the arrival of people in the landscape (Urrego et al., 2011). Human activities provided a source of fire ignition in the area, which extends to today and prevents expansion of the woodlands after their 'natural' suppression during the HDE. It is therefore apparent, that *Polylepis* has developed a natural resilience to aridity (persisting in small ecological niches) but is not necessarily adapted to endure elevated human impacts which effectively cut the natural cycle of woodland expansion and contraction.

The palaeoecological record can also provide information on the impact of landscape degradation by human activity, (*i.e.* where woodland taxa are not sufficiently resilient to withstand the climate and human stresses). At LC human populations responded to changes in resource availability by switching from the collection and burning of fuelwood, to the utilization of dried dung as camelid numbers in the area increased rapidly (Chapter 4; Williams et al., 2011). Dried cattle/camelid dung has long provided an alternative fuel to wood fires (Janusek, 2008), and in many rural Andean regions today dung acts as an important energy source and in Bolivia accounts for 19% of total biofuel use (Winterhalder et al., 1974; World Bank, 1994; Yevich and Logan, 2003). This cultural adjustment at c. 1,300-1,000 cal yr BP had apparently no major detrimental effects on the human population of the area (*e.g.* no abandonment) and may have possibly even had positive effects, as the time spent gathering fuel wood could be allocated to other tasks (Chapter 4; Williams et al., 2011).

### *Lake macro-invertebrates*

From the analysis of subfossil chironomids from the sediments of LKKU and LC, the decline of *Cricotopus* / *Orthocladius* type in LKKU from c. 6,500 cal yr BP is a key shift observed in the record (Chapter 6; Figure 6.4). Throughout the previous 12,000 years, this taxon had been continually present at the LKKU, through periods of regionally recognised temperature amelioration and decreasing wetness. Even during the height of the HDE, *Cricotopus* / *Orthocladius* persisted, as did all other taxa identified in the record (Figure 6.4). However, a rapid onset of wetter conditions marked by an expansion of marsh woodland (*Alnus*) at lower elevations, and a fire frequency decline, coincided with a decline in *Cricotopus* / *Orthocladius* from the lake after c. 6,500 cal yr BP. Because of the infancy of chironomid research in Bolivia, and generally across the Andes (Section 6.2), causes for this decline are speculative. However, there is no indication of any human impact at the site during this time (Chapter 5) and, with the evidence available, this shift in the chironomid assemblage appears linked to moisture increase and the associated impacts of lake deepening and increased in-wash. These findings are further indication that moisture is a key driver of biotic organisation in the Tropical Andes.

## **7.5) Implications**

### **7.5.1) Conservation and vulnerability**

Undisturbed super-humid locations in Tropical Andes have been identified as critical for conservation targets due to the high biodiversity they maintain (Section 7.1.1; Killeen et al., 2007). Evidence from the palaeo-records from the Cochabamba Basin suggests that moisture balance does indeed underpin the spatial variation in biodiversity (Chapters 4–6). Therefore, while the palaeoecological data support the interpretation that conservation of these “wet spots” is important, it should not be at the expense of those areas which are already impacted by humans. Indeed, some plant species thrive in disturbed landscapes (Kessler, 1999) and there is a close relationship between avian biodiversity and ancient population centers, which possibly stimulated the development of rich, co-adapted, species and communities (Fjeldså, 2007).

The protection of sites such as LKKU are likely to be deemed more important to non-local groups due to the current, more natural status of the associated ecosystems, often a result of remoteness and limited accessibility. However, the management at sites such as LC and the Vacas Lake District are more valuable to local populations. These locations pose a greater conservation challenge as policy must balance biodiversity and yet continue to support a population that, as with the whole Andes, is expected to increase in the future. Maintaining ecosystem services requires careful assessment of the ecology and examination of the complex impacts of increasing human populations. For example, increasing water shortages due to growing populations will deplete the freshwater input to valuable lakes such as LC, limiting the provision of drinking water and food (aquatic vegetation) important for cattle (Section 4.2.1).

The adaptability of human populations is also apparent in the palaeoecological records. As well as highlighting how ecosystems, communities and species adjust to environmental changes, the palaeoecological data also shows that past human populations are able to absorb changes occurring in the landscape and adapt practices accordingly. Examples of such adjustments include: i) switching fuel source (Chapter 4; Williams et al., 2011), and ii) developing agroforestry (Chepstow-Lusty and Winfield, 2000). However, in order to facilitate future adjustments it is essential that the opportunity and ability of both ecosystems and people to adapt is maintained.

### **7.5.2) The future of *Polylepis* woodlands**

Considering the ecosystems services provided by *Polylepis* woodlands for the communities of the high Andes (Section 7.3.1), it is imperative that their importance is highlighted to landowners. If the benefits of woodland protection can be promoted, local forest stewardship can result in improving ecosystem services whilst simultaneously supporting the local biodiversity.

The palaeoecological data discussed here demonstrates that if given the opportunity, following times of unfavourable conditions, *Polylepis* woodlands will recover and their history of expansion and contraction as climate changes, highlights the woodland's resilience (Chapter 5; Section 7.4.3). As previously discussed, there is evidence from

palaeo-records and non-palaeo research that highlights the need for the protection of niche space and physical features over the transient species and communities that inhabit them (see Section 7.2). For high Andean *Polylepis* woodland this is also crucial, as there is need to maintain features such as boulderfields, scree slopes and protected gulleys which act as natural fire breaks allowing *Polylepis* to remain locally present even during the most unfavourable climatic times (chapter 5). However, there is no evidence that other tree/shrub communities expanded to fill the niche-space made available when *Polylepis* woodland was most restricted (Figure 5.4). In contrast, grasses, which have already been shown to be abundant on the landscape, appear to have been the main beneficiary of a reduction in woodland. With high Andean woodland clearly crucial for supporting biodiversity and for providing ecosystem services to local human populations, and with no other arboreal taxa able to survive in such harsh environments as *Polylepis*, there is justification for a species-based, as well as niche-based, conservation approach. Ultimately, removal of *Polylepis* woodland, either by natural landscape transformative processes (e.g. aridity-initiated fire) or by more selective human processes (e.g. cutting for timber or fuel), will reduce the biodiversity of the area.

To address the importance of *Polylepis* woodlands in supporting biodiversity, land managers in the high Bolivian Andes are already encouraged to use *Polylepis* over exotic tree species for the control of erosion and for the provision of firewood (Fjelds  and Kessler, 1996). While this practice should continue, land managers must start to take into account the findings established from local and regional palaeoecological records. Current projects such as the Asociaci n Ecosistemas Andinos (ECOAN) in Peru have initiated the planting of 60,000 *Polylepis racemosa* trees, in a direct attempt to join up fragments of existing woodland (Aucca and Ramsay, 2005). But if the ultimate conservation aim is to restore the natural ecosystem state, we must “mimic” the vegetation structure seen in the palaeoecological records.

From the currently available records across the eastern central Andes, there is no evidence that *Polylepis* woodland ever formed a continuous forest habitat (Chapters 4 and 5). This suggests that even in the absence of human impacts, woodlands always remained in isolated stands within an Andean grassland matrix. Planting project such as

ECOAN, which aim to link up woodland patches, take no account of how the modern vegetation structure was formed. Indeed, it has been shown that species endemism is highest at woodland patches and not in the continuous forest belts (Fjeldså and Irestedt, 2009) and so linking up woodland patches may actually be detrimental to the overall biodiversity.

## **7.6) Conclusions**

Palaeoecological data are a valuable source of information for conservation-related questions and provide a tool which can provide data relevant for policy makers. However, to determine conservation priorities, objectives must already be set (e.g. maintain as much naturalness as possible, help balance human-environment interactions, or provide much needed resources). Assessing local risks to vulnerable biotopes is crucial and one which conservation policy makers must engage with local people. However, background information regarding the impact and duration of past human intervention there has been in an area is also essential and there is urgent need for evidence-based conservation. In this respect, the multi-proxy analysis of palaeo-records, such as those presented in this research, are fundamental for conservations managers who must make informed decisions based on the data available to them from across the whole scientific community.



## **Chapter 8) Conclusions**

In this chapter, the main findings of the thesis are summarised. First, the thesis rationale is reviewed before concluding remarks are made specifically addressing the original research goals outlined. Secondly, suggestions for future work and further application of this research are discussed.

---

### **8.1) Summary of thesis rationale and objectives**

Population growth and predicted global climate change are applying new, and increasing, pressure to Andean environments, but the consequences of these changes upon the biodiverse and vulnerable Tropical Andean ecosystems are poorly understood. Past environmental shifts can be used to obtain empirical data that demonstrates how these ecosystems are likely to respond to future change. Via the use of palaeolimnological studies, the sensitivity of the Tropical Andean ecosystems to historical environmental changes allows the evaluation of long-term ecological adjustments.

The last c. 21 ka is a critical time period for understanding human and climate interactions in the Andes because it contains: i) the last major global climatic change (full glacial to interglacial transition, and ii) the arrival and subsequent spread of humans throughout South America (see Chapter 1). The deglaciation period and early Holocene represents the most recent time when the ecosystems of the Tropical Andes were not substantially influenced by human practices, but were exposed to naturally varying ecological stress levels. The subsequent development of human culture through the Holocene lead to changes in resource uses and practices, such as land use change, agricultural and animal domestication, which placed a unique set of pressures upon the ecosystems they occupied.

Due to the complex human-climate-ecosystem interactions (Chapters 1 and 3), a history of climatic changes and human impacts is essential before we can fully understand the threats imposed upon ecosystems today, and demonstrate how they are likely to respond to future change. However, the history of the Tropical Andes, as with much of the

Neotropics is still insufficiently understood and fragmentary due to a paucity and uneven spread of archaeological and palaeoenvironmental records. The correlation of changing environments and human cultures, together with assessing the scale and nature of human-environment interactions, is an important issue that warrants continued discussion and debate.

The intent of this thesis was to improve understanding of human-ecosystem-climate interactions by tracing Tropical Andean ecosystem adjustments of the past using the sediment records from two lakes in the eastern Bolivian Andes. How the three specific research aims, detailed in Chapter 1 (Section 1.3) and reproduced below, have been addressed are summarised in the following sub-sections.

The research aims were:

- i. To determine the scale and impact of climatic events, climate system adjustments and ecosystem responses in the Bolivian Andes since deglaciation, and to examine the uniformity and correlation of these changes to other Andean locations.
- ii. To determine how pre-Columbian population enclaves, distant from the civilization centres of Cusco and Tiwanaku, impacted the landscape that they occupied, via the exploitation of agricultural development, domestication of animals and fire. To examine if these impacts were wholly detrimental to the biodiversity of the Tropical Andean region in which they existed.
- iii. To assess the drivers governing the current distribution of *Polylepis* woodland and Andean grassland, and determine if the historic growth patterns suggests a previous, more widespread dominance. To provide new data useful for conservation policies and management strategies to assist with the replication of the natural ecosystem structure.

## **8.2) Specific research findings**

### **8.2.1) The scale and impact of climatic adjustments**

- i. To determine the scale and impact of climatic events, climate system adjustments and ecosystem responses in the Bolivian Andes since deglaciation, and to examine the uniformity and correlation of these changes to other Andean locations.*

The complete paleolimnological histories of Laguna Khomer Kotcha Upper and Lake Challacaba have revealed that ecosystem adjustments in the Cochabamba Basin, Bolivia, have been driven by climatic factors during the last c. 18 ka (Chapters 4-6). The multi-proxy analysis, particularly the combination of pollen, charcoal and chironomid assemblages, has, for the first time, identified biological changes within the lake system and in the local and regional terrestrial vegetation of the eastern Bolivian Andes. This research has explored the sensitivity of the preserved ecological markers (fossil pollen, spores, charcoal, chironomids) in the detection of both major and subtle environmental changes, including temperature, net moisture availability and the associated variations in vegetation, fire regime, water level and salinity.

The sediment record from Laguna Khomer Kocha Upper, dating back c. 18 ka cal BP shows that climatic variation and the associated changes in fire regime, have long been a transformative agent of local and regional vegetation in the high Andes. The deglaciation period during the Late Pleistocene (c. 18-10 ka cal BP), was a relatively gradual climatic transition in the eastern Andean flanks (Section 5.6.1). In contrast to palaeo-records from the Altiplano, as discussed in Sections 1.1.3, there is no evidence for the occurrence of globally known climatic events such as an interstadial or Younger Dryas-type stadial in the proxy data from Laguna Khomer Kocha Upper (Section 5.6).

The onset of the fire activity from c. 14.5 ka cal BP, with a major increase at c. 10.1 ka cal BP (Section 5.6.2), steadily transformed the local vegetation (*i.e.* decreased abundance of high elevation woodland) but had only minor impacts on lake biota (Section 6.6.2). The change in burning regime was driven by an increase in regional climate aridity, and the fluctuations observed confirms that the Holocene dry event was multi-millennial in

duration (c. 10.1–6.4 ka cal BP) and was punctuated by episodic wet phases (Section 5.6.2). In contrast to other central Andean lake basins, the continuation of the ascending ground-level cloud cover from lower elevations was sufficient to maintain an inundated lake basin at Khomer Kocha, highlighting both the importance and spatial variation in Amazon derived moisture input (Chapter 5). Increased moisture availability at c. 6.4 ka cal BP, caused a decline in burning, a rapid adjustment in local and lower elevation vegetation (Section 5.6.3) and an increase in lake depth (Section 6.6.2; Figure 6.5). This onset of generally wetter conditions concurs with the timing of similar adjustments at other eastern Andean locations (as discussed in Chapter 5).

From the 4 ka cal BP record of lake Challacaba, fluctuations in the abundance of drought tolerant plants (e.g. Caryophyllaceae, Chenopodiaceae/Amaranthaceae; Chapter 4; Figure 4.), shifts in chironomid assemblages (Section 6.6.1.; Figure 6.4) and variation in the geochemical data (Figure 4.3), indicate two periods of reduced moisture availability and increase salinity (c. 4–3.3 and c. 2.1–1 ka cal BP) compared to adjacent wetter episodes (c. 3.3–2.1 and c. 1 ka cal BP to the present day). These moisture fluctuations can be correlated to variations in the El Niño/Southern Oscillation. The aridity before c. 3.3 ka cal BP is also linked to the latter stages of the region wide Holocene dry event (Chapter 4; Williams et al., 2011). As previously discussed, the timing of lake formation at Lake Challacaba, is concomitant with those seen in other dry, inter-Andean locations across the Andes (Section 4.5.1). However, in comparison to the closest alternative study site, Laguna Khomer Kotcha Upper (35 km north), the occurrence and timing of climatic adjustments are non-uniform. This finding highlights the spatial variation of climatic change and ecosystem vulnerability in the biodiversity hotspot of the Tropical Andes, a factor of the heterogeneity induced by the complex Andean topography (Chapter 7).

As well as recording the environmental history of local vegetation dynamics, long-distance pollen transport provides evidence of changes in more distal vegetation zones. At Laguna Khomer Kotcha Upper, the sensitivity of the lower elevation montane forests to burning regime changes is identified (Chapter 5). The simultaneous changes in both Andean (local) and lowland (distal) taxa (Figure 5.4), suggests that vegetation dynamics in the two environments can be linked to a common climatic driver.

### 8.2.2) Pre-Columbian populations

- ii. *To determine how pre-Columbian population enclaves, distant from the civilization centres of Cusco and Tiwanaku, impacted the landscape that they occupied, via the exploitation of agricultural development, domestication of animals and fire. To examine if these impacts were wholly detrimental to the biodiversity of the Tropical Andean region in which they existed.*

With the limited number of archaeological sites in, and around, the Cochabamba Basin, this thesis has provided important new findings relevant to expanding the current knowledge of pre-Columbian cultures (*i.e.* those present in South America prior to the arrival of Christopher Columbus during AD 1492). The research presented here has explored patterns of perceived vegetation change attributed to human activity (*i.e.* landscape exploitation), and suggests how ancient human populations may have responded and adapted to environmental change (Chapter 4; Williams et al., 2011).

The multi-proxy analysis of the sediments from Lake Challacaba has revealed the importance of the Vacas Lake District as a site of human occupation during the last c. 4 ka (Chapter 4; Williams et al., 2011). Although the ancient road network passing through the Vacas district had previously been identified as important during Incan times (c. 0.6-0.5 ka cal BP), little was known about the longevity or history of this trade route (Sections 1.4.4 and 4.2.1). From the examination of fossil pollen and spores (e.g. the dung fungus *Sporormiella*) from the Lake Challacaba record (Chapter 4; Williams et al., 2011; Figure 4.4), this research provides evidence indicating that the road network was in use by at least c. 1.2 ka cal BP, suggesting that Andean and lowland areas were connected, by trade routes through the Cochabamba valleys, before the end of Tiwanaku state (1.5–0.9 ka cal BP).

The charcoal record indicates that the local ecosystem has been under anthropogenic influence for the duration of the Challacaba record (c. 4 ka; Figure 4.4). Despite the presence of human activity, there appears to have been no decline in highly sought-after wood resources (e.g. *Polylepis* and *Alnus*) regularly documented in many other Andean

records (Section 4.5.4). This has highlighted the danger of directly linking human presence in the landscape with degradation of high Andean ecosystems (Section 7.4).

A marked change in the preserved ecological assemblages between c. 1.3 and 1 ka cal BP, has been one of the most intriguing findings of the Challacaba record and of this thesis as a whole (Section; 4.5.6; Figure 4.4). A decline in charcoal and an increase in camelid numbers (*Sporormiella*), lake nutrient input and landscape disturbance (*Pediastrum* and Chironomidae), and the arrival of an invasive plant (*Ludwigia*), indicate elevated pastoral agriculture from this time (Chapters 4 and 6). The timing of this shift is broadly coeval with the fragmentation and later collapse of the Tiwanaku state (c. 1000-900 cal yr BP), which is linked to prolonged drought on the Altiplano (Section 1.1.4). The data from the Challacaba record, demonstrates that the development and fragmentation of the Tiwanaku civilisation had knock-on-effects for the distance populations in the Cochabamba Basin, providing strong evidence that this region was under Tiwanaku control and within their sphere of influence (Chapter 4; Williams et al., 2011).

In summary, the ecological assemblages (pollen, spore, charcoal, algal and chironomid) from the Lake Challacaba record during the last 1 ka differ to those from any other time during the preceding 3 ka. This environmental change is likely to be associated to cultural adjustments lead by the development and subsequent declines of the Tiwanaku and Inca states (as discussed in Section 1.1.4). Over this period, we also have an indication of how human populations adapted to changing conditions and were able to utilise new, readily available, resources, such as the inferred increase in the use of camelid dung as a fuel source (Sections 4.5.3 and 7.7.4.3). In addition, the landscape scale spatial variability of change within the Andes has been explored (Chapter 7). While the effects of human impact were obvious at Lake Challacaba, there is no evidence for their impacts in the environment around Laguna Khomer Kotcha Upper during the entire duration of the recovered record (c. 18-1 ka cal BP; Section 7.4.1). Although the lack of a human occupation signal at the this site limits the conclusions that can be made regarding pre-Columbian impacts on the moist eastern ranges, it does signify the importance of Laguna Khomer Kocha Upper in providing a record of vegetation response to climate without anthropogenic influence, a rare situation in Tropical Andean palaeoecological records.

### 8.2.3) The natural history of the *Polylepis* woodlands

- iii. *To assess the drivers governing the current distribution of Polylepis woodland and Andean grassland, and determine if the historic growth patterns suggests a previous, more widespread dominance. To provide new data useful for conservation policies and management strategies to assist with the replication of the natural ecosystem structure.*

As *Polylepis* woodlands are such an important component of the high Andean ecosystems of Bolivia (Sections 1.1.2 and 7.3.1) they have had a prominent role in the discussions throughout this thesis (Chapters 1–8). The analysis of the c. 18 ka cal BP sediment record from Laguna Khomer Kocha Upper (Chapter 5), demonstrated that fire regimes were critical in determining the niche-space available for *Polylepis* woodland growth and that fire has long been a transformative agent of eastern Andean vegetation as a whole (Section 5.6). In a local environment free from human intervention, fire, controlled by climatic aridity, facilitated the expansion and contraction of *Polylepis* woodland patches in a landscape otherwise dominated by Andean grassland (Figure 5.4).

While there can be no doubt that in recent times (*i.e.* last 50 years) human practices are, in general, detrimental to *Polylepis* woodland (Sections 1.1.2 and 7.3.1), harmful human impacts over longer time scales are more variable. High resolution analysis of the last four millennia from the sediments Lake Challacaba shows non-uniform human impacts, both in occurrence and effect. Also at Lake Challacaba, there is no evidence that human occupation in the Vacas area resulted in either abrupt or gradual woodland clearance (Chapter 4; Williams et al., 2011).

The palaeoecological data presented in this thesis supports a conclusion that, during the last 18 ka, *Polylepis* woodlands never formed a continuous forest belt at high elevations (> 3000 m asl) in the eastern Bolivian Andes. Contrary to perceived ecological understanding (see Section 1.1.2), the palynological data from Laguna Khomer Kocha Upper and Lake Challacaba both suggest that the woodlands maintained a patchy distribution both before and during human arrival (Chapter 4 and 5). There is no

indication that human impact alone was responsible for creating the woodland structure observed today. Instead, palaeoecological analysis of the sediments from Laguna Khomer Kocha Upper highlights the role of *Polylepis* woodland's long-term sensitivity to fire regime and moisture availability and identifies these as the key drivers of the woodland/grassland matrix (Section 5.6).

The importance of maintaining woodland patches for biodiversity and ecosystem services, both near and remote from human populations, has been identified from the literature (Section 1.1.2) and extensively discussed in this thesis (Chapter 7). This research supports the importance of *Polylepis*, by highlighting its unique resilience and ability to survive under harsh environmental conditions that are associated to the high elevations of the eastern Andes (Section 7.3.4). The palynological data shows, that in these harsh environments, no other arboreal taxon was able to replace *Polylepis* woodland when its abundance was reduced (Chapter 5; Figure 5.4). These findings have major implications for conservation, as loss of high elevation woodland would have severe consequences for the biodiversity of the associated plants, birds and mammals supported (see Section 1.1.2). Therefore, there is clear justification for a species-based, as well as niche-based, conservation approach (Section 7.5.2).

Although justifying a species-based conservation approach and supporting the ongoing *Polylepis* re-establishment projects underway in the Andes (e.g. ECOAN; Section 7.5.2), the palaeoecological data from the Laguna Khomer Kocha Upper and Lake Challacaba study sites has provided new baseline data of woodland distribution patterns. These data indicate that the woodlands never formed a continuous habitat and therefore planting strategies, such as ECOAN, must aim to recreate and mimic the natural patchy distributions observed from the palaeoecological records (as discussed in Section 7.5.2).



### **8.3) Suggestions for future work**

#### **8.3.1) Data collection**

Much progress has been made over recent decades in the identification and interpretation of Andean/Amazonian pollen records, including the modern transport mechanisms and the spectra typical of a variety of tropical ecosystems (Sections 1.2 and 3.4.1; Chapters 4 and 5). However, as highlighted by this thesis, the paucity of modern autecological chironomid data and taxonomic keys for the Andes remains a large stumbling block in the interpretation of subfossil Chironomidae from paleolimnological records (Section 6.2). As demonstrated by this research, at present, subfossil chironomid analysis has to be combined with other proxy data (e.g. palynological, charcoal and geochemical) that quantify the variables in order to provide meaningful conclusions (Section 6.6.3). However, data presented here (Section; 6.5; Figures 6.4 and 6.5) suggest that changes in the chironomid assemblages can indicate environmental changes not detected by other proxies. Therefore, a research focus must be developed to advance the analysis and interpretation of subfossil Chironomidae from the central Andes of Bolivia/Peru. Primary steps in addressing the current knowledge gap must include: i) an inventory of species present in central Andean water bodies, and ii) the association of these species to water properties, terrestrial climatic conditions and lake basin vegetation. Examining the distribution of species under modern conditions will unlock the full potential of subfossil chironomid analysis and allow researchers to pursue a previously under exploited tool in the examination of new and existing palaeoenvironmental records from the region.

Perhaps one of the more obviously lines of future research, which will build upon the findings of this thesis, is the extraction of longer and more complete limnological records from the study region. The sediment cores obtained from Lake Challacaba have provided a detailed analysis of human-climate-vegetation interactions over the past 4 ka highlighting that the Vacas Lake District was an important location on a pre-Columbian roadway network (Chapter 4; Williams et al., 2011). However, preliminary investigation at the other lakes in the area indicate that a much longer record is likely to be available (Section 1.4.1; Table 1.2; Figure 2.1). The deep (>13 m) glacial scour lake of Acerokocha, 3 km west of Lake Challacaba, is anticipated to contain a record dating from at least the last

glacial maximum (c. 21 ka cal BP). Analysis of the surface sediments from Acerokocha have already revealed that chironomid and pollen is persevered (not shown in the thesis), and with the lake easily accessible by an off-road vehicle, a coring attempt should be made a future priority. Obtaining a record of equal length to Laguna Khomer Kocha Upper from the Vacas Lake District would allow new and fuller comparisons to be made between two sites dominated by opposing geographic location, precipitation regimes and human histories. Extending the record from the Vacas Lake District would also allow testing the conclusion made in this thesis: that no large scale *Polylepis* clearance occurred with the arrival of humans. With a scarcity of pre-Incan archeological sites in Bolivia (see Sections 1.1.4 and 1.4.4), the examination of palaeoenvironmental records has the potential to continue to fill a void in our knowledge of how early humans adapted to changing environmental conditions and how they may have shaped the modern landscape.

Obtaining additional sedimentary records from the surrounds of Laguna Khomer Kocha Upper should also be a future target. As the uppermost 1 ka of sediment could not be collected from the lake itself during the fieldwork of 2007, returning with additional surface sampling equipment may allow these sediments to be captured. An alternative for obtaining this recent time-period would be to core the area of waterlogged ground adjacent to the lake (see Section 2.2.1; Figure 2.6). Tracing the environmental history through the last 1 ka would allow better understanding of the recent vegetation dynamics and provide a pollen spectra that can be directly related to the modern *Polylepis* woodland structure and abundance. The surprisingly long record extracted from Laguna Khomer Kocha Upper (413 cm; c. 18,000 ka cal BP), suggests that older sediments could possibly be contained within the larger and deeper (>10 m) basin of Laguna Khomer Kocha (Lower), situated at 3900 m above sea level (Sections 1.4.1 and 2.2.1; Table 1.2; Figure 2.6). Even if the sediment record from this lower site only extends to a similar time, the comparison between the locations could potentially allow assessments such as plant migration rates, pollen transport mechanisms and the scale of burning events.

### **8.3.2) Data application**

Examining the natural and human histories of Lake Challacaba and Laguna Khomer Kocha Upper has revealed how the vulnerabilities of each site are ultimately driven by the complex topography of the eastern Andes (Chapter 7). Moisture balance and environmental stability was shown to underpin the biodiversity of each location, and also influence human settlement over very small spatial scales. With several other pairs of lakes existing along the length of the Andes (Ecuador and Peru) which are situated in opposing dry and wet spots, there is the opportunity to further investigate these findings by using the palaeoecological records already extracted from these sites. If differences in climatic stability of these sites in the past, due to their geographic setting, can be associated to the vulnerability of each location today, there are major implications for conservation strategies. Comparison of long-term climatic stability at these sites will help to further assess the vulnerabilities of these locations to climatic changes predicted regionally. Developing a fuller understanding of the importance of spatial scale and a better knowledge of the impacts of global versus local scale environmental changes, will assist ecological conservation management in these biodiverse areas.

The early warning potential of mountain regions is yet to be fully appreciated or understood. Although this thesis represents a significant forward step, the future research targets outlined above would continue to address unresolved questions and lead to better understanding of human and climatic threats upon the biodiverse Tropical Andes. Continuing to learn lessons from the past provides a rare opportunity to examine how these valuable ecosystems are likely to cope with future environmental change. Palaeoenvironmental data provides a means in which to examine the long-term response of ecosystems through not only naturally varying ecological stress levels, but also through times of changing human cultural development, examining the amplitude of changes, lag times and tipping points. Such data helps to produce better conservation and resource strategies, assisting the preservation of the unique ecological wealth and helping to secure the future of regionally growing human populations.

## References

- 
- Abbott, M.B., Binford, M.W., Brenner, M. and Kelts, K.R., 1997. A 3500  $^{14}\text{C}$  yr high-resolution record of water-level changes in Lake Titicaca, Bolivia/Peru. *Quaternary Research* 47, 169-180.
- Abbott, M.B., Wolfe, B.B., Wolfe, A.P., Seltzer, G.O., Aravena, R., Mark, B.G., Polissar, P.J., Rodbell, D.T., Rowe, H.D. and Vuille, M., 2003. Holocene paleohydrology and glacial history of the central Andes using multiproxy lake sediment studies. *Palaeogeography, Palaeoclimatology, Palaeoecology* 194, 123-138.
- Adger, W.N., 2006. Vulnerability. *Global Environmental Change* 16, 268-281.
- Ahmed, S.I. and Cain, R.F., 1972. Revision of the genera *Sporormia* and *Sporormiella*. *Canadian Journal of Botany* 50, 419-477.
- Albarracin-Jordan, J., 1992. Prehispanic and early Colonial settlement patterns in the Lower Tiwanaku Valley, Bolivia. Unpublished Ph.D. thesis. South Methodist University, Dallas.
- Aldenderfer, M., 2009. Key research themes in the South-Central Andean Archaic. In: Marcus, J. and Williams, P.R. (Eds.), *Andean Civilization: a tribute to Michael E. Moseley*. Cotsen University of Archaeology Press, UCLA, pp. 75-88.
- Ali, A.A., Higuera, P.E., Bergeron, Y. and Carcaillet, C., 2009. Comparing fire-history interpretations based on area, number and estimated volume of macroscopic charcoal in lake sediments. *Quaternary Research* 72, 462-468.
- Alley, R.B. and Ágústssdóttir, A.M., 2005. The 8k event: cause and consequences of a major Holocene abrupt climate change. *Quaternary Science Reviews* 24, 1123-1149.
- Araneda, A., Cruces, F., Torres, L., Bertrand, S., Fagel, N., Treutler, H., Chirinos, L., Barra, R. and Urrutia, R., 2007. Changes of sub-fossil chironomid assemblages associated with volcanic sediment deposition in an Andean lake (38°S), Chile. *Revista Chilena de Historia Natural* 80, 141-156.
- Arce-Burgoa, O.R., 2009. Metalliferous ore deposits of Bolivia. SPC Impresores, La Paz.
- Arce-Burgoa, O.R. and Goldfarb, R.J., 2009. Metallogeny of Bolivia. *Society of Economic Geologists Newsletter* 79, 7-15.

- Argollo, J. and Mourguiart, P., 2000. Late Quaternary climate history of the Bolivian Altiplano. *Quaternary International* 72, 37-51.
- Argollo, J., Solís, C. and Villalba, R., 2006. History of high mountain forests of *Polylepis tarapacana* at the Bolivian Central Andes. In: (Kaufmann, V. and Sulzer, W (Eds.), *Proceedings of the 8th International Symposium on High Mountain Remote Sensing Cartography*. Karl Franzens University, Graz, pp. 9-16.
- Armitage, P.D., Cranston, P.S. and Pinder, L.C.V., 1995. *The Chironomidae: Biology and ecology of non-biting midges*. Chapman and Hall, London.
- Ashe, P., Murray, D.A. and Reiss, F., 1987. The zoogeographical distribution of Chironomidae (Insecta: Diptera). *Annales de limnologie* 23, 27-60.
- Aucca, C. and Ramsay, P.M., 2005. Management of biodiversity and land use in southern Peru. *Mountain Research and Development* 25, 287-289.
- Ayala, R., Acosta, F., Mooij, W., Rejas, D. and Van Damme, P., 2007. Management of Laguna Alalay: a case study of lake restoration in the Andean valleys in Bolivia. *Aquatic Ecology* 41, 621-630.
- Bader, M.Y., 2007. Tropical alpine treelines: how ecological processes control vegetation patterning and dynamics. Unpublished Ph.D. thesis. Wageningen University, Wageningen.
- Baker, P.A., Bush, M.B., Fritz, S., Rigsby, C.A., Seltzer, G. and Silman, M., 2003. Last Glacial Maximum in an Andean cloud forest environment (Eastern Cordillera, Bolivia): Comment and Reply. *Geology* 31, 26-27.
- Baker, P.A., Rigsby, C.A., Seltzer, G.O., Fritz, S., Lowenstein, T.K, Bacher, N.P and Veliz, C. 2001a. Tropical climate changes at millennial and orbital timescales on the Bolivian Altiplano. *Nature* 409, 698-701.
- Baker, P.A., Seltzer, G.O., Fritz, S.C., Dunbar, R.B., Grove, M.J., Tapia, P.M., Cross, S.L., Rowe, H.D. and Broda, J.P., 2001b The history of South American tropical precipitation for the past 25,000 years. *Science* 291, 640-643.
- Bandy, M.S., 2004. Fissioning, scalar stress, and social evolution in early village societies. *American Anthropologist* 106, 322-333.
- Barbier, E.B., 1997. The economic determinants of land degradation in developing countries. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 352, 891-899.

## References

- Barnett, T.P., Adam, J.C. and Lettenmaier, D.P., 2005. Potential impacts of a warming climate on water availability in snow-dominated regions. *Nature* 438, 303-309.
- Bazzaz, F.A., 1996. *Plants in changing environments: linking physiology, population and community ecology*. Cambridge University Press, Cambridge.
- Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. *New Phytologist* 132, 155-170.
- Bennett, K.D. and Willis, K.J., 2001. Pollen. In: Smol, J.P., Birks, H.J.B. and Last, W.M. (Eds.) *Tracking environmental change using lake sediments. Volume 3: Terrestrial, algal, and siliceous indicators*. Kluwer Academic Publishers, Dordrecht, pp. 5 -32.
- Berger, T., Mendoza, J., Francou, B., Rojas, F., Fuertes, R., Flores, M., Noriega, L., Ramallo, C., Ramirez, E. and Baldivieso, H., 2005. Glaciares Zongo – Chacaltaya – Charquini Sur. Bolivia 16°S. Mediciones Glaciológicas, Hidrológicas & Meteorológicas. Año hidrológico 2004-2005. Informe Great Ice Bolivia, IRD-IHH-SENAMHI-COBEE, La Paz.
- Bervoets, L., Solis, D., Romero, A.M., Damme, P.A.V. and Ollevier, F., 1998. Trace metal levels in chironomid larvae and sediments from a Bolivian river: impact of mining activities. *Ecotoxicology and Environmental Safety* 41, 275-283.
- Bigler, C., Heiri, O., Krskova, R., Lotter, A. and Sturm, M., 2006. Distribution of diatoms, chironomids and cladocera in surface sediments of thirty mountain lakes in south-eastern Switzerland. *Aquatic Sciences: Research Across Boundaries* 68, 154-171.
- Binford, M.W., Kolata, A.L., Brenner, M., Janusek, J.W., Seddon, M.T., Abbott, M. and Curtis, J.H., 1997. Climate variation and the rise and fall of an Andean civilization. *Quaternary Research* 47, 235-248.
- Birks, H.J.B., 1985. Recent and possible future mathematical developments in quantitative palaeoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 50, 107-147.
- Birks, H.J.B., 1996. Contributions of Quaternary palaeoecology to nature conservation. *Journal of Vegetation Science* 7, 89-98.
- Birks, H.J.B. and Birks, H.H., 1980. *Quaternary Palaeoecology*. Edward Arnold, London.
- Birks, H.J.B., 1998. Numerical tools in palaeolimnology: progress, potentialities and problems. *Journal of Paleolimnology* 20, 307-332.

- Birks, H.J.B. and Birks, H.H., 2006. Multi-proxy studies in palaeolimnology. *Vegetation History and Archaeobotany* 15, 235-251.
- Birks, H.J.B. and Gordon, A.D., 1985. Numerical methods in Quaternary pollen analysis. Academic Press, London.
- Bitter, G., 1911. Revision der Gattung *Polylepis*. *Botanische Jahrbücher für Systematik* 45, 564-656.
- Björck, S. and Wohlfarth, B., 2001.  $^{14}\text{C}$  Chronostratigraphic techniques in paleolimnology. In: Smol, J.P., Birks, H.J.B and Last, W.M. (Eds.), *Tracking environmental change using lake sediments: Volume 1: basin analysis, coring and chronological techniques*. Kluwer Academic Publishers, Dordrecht, pp. 205-245.
- Blackford, J.J., 2000. Charcoal fragments in surface samples following a fire and the implications for interpretation of subfossil charcoal data. *Palaeogeography, Palaeoclimatology, Palaeoecology* 164, 33-42.
- Blard, P.H., Lavé, J., Farley, K.A., Fornari, M., Jiménez, N. and Ramirez, V., 2009. Late local glacial maximum in the Central Altiplano triggered by cold and locally-wet conditions during the paleolake Tauca episode (17-15 ka, Heinrich 1). *Quaternary Science Reviews* 28, 3414-3427.
- Blossey, B., 1999. Before, during and after: the need for long-term monitoring in invasive plant species management. *Biological Invasions* 1, 301-311.
- Blum, P., 1997. Physical Properties Handbook: a guide to the shipboard measurement of physical properties of deep-sea cores. ODP Technical Note 26, [Online]. DOI:10.2973/odp.tn.26.1997.
- Bond, G., Broecker, W., Johnsen, S., McManus, J., Labeyrie, L., Jouzel, J., and Bonani, G., 1993. Correlations between climate records from North Atlantic sediments and Greenland ice. *Nature* 365, 143-147.
- Borror, D.J., DeLong, D.M. and Triplehorn, C.A., 1976. An introduction to the study of insects. Holt, Rinehart & Winston, Toronto.
- Bräuning, A., 2009. Climate variability of the Tropical Andes since the late Pleistocene. *Advances in Geosciences* 22, 13-25.

- Brenner, G.J., 1996. Evidence for the earliest stage of angiosperm pollen evolution: a paleoequatorial section from Isreal. In: Taylor, D.W. and Hickey, L.J. (Eds.), Flowering plant origin, evolution and phylogeny. Chapman and Hall, New York, pp. 91-115.
- Brenner, M., Rosenmeier, M.F., Hodell, D.A. and Curtis, J.H., 2002. Paleolimnology of the Maya lowlands: long-term perspectives on interactions among climate, environment, and humans. *Ancient Mesoamerica* 13, 141-157.
- Brodersen, K.P., 2008. Book Review of: Brooks, S.J., Langdon, P.G. and Heiri, O., 2007. The identification and use of palaeartic Chironomidae larvae in palaeoecology. QRA Technical Guide No. 10. Quaternary Research Association, London. *Journal of Paleolimnology* 40, 751–753.
- Brodersen, K.P. and Quinlan, R., 2006. Midge as palaeoindicators of lake productivity, eutrophication and hypolimnetic oxygen. *Quaternary Science Reviews* 25, 1995-2012.
- Brodin, Y.W. and Gransberg, M., 1993. Responses of insects, especially Chironomidae (Diptera), and mites to 130 years of acidification in a Scottish lake. *Hydrobiologia* 250, 201-212.
- Brooks, S.J., 2005. Chironomid analysis to interpret and quantify Holocene climate change. In: Mackay, A., Battabee, R., Birks, H.J.B. and Oldfield, F (Eds.), *Global change in the Holocene*. Arnold, New York, pp. 329 - 341.
- Brooks, S.J., 2000. Late-glacial fossil midge stratigraphies (Insecta: Diptera: Chironomidae) from the Swiss Alps. *Palaeogeography, Palaeoclimatology, Palaeoecology* 159, 261-279.
- Brooks, S.J., Bennion, H., and Birks, H.J.B., 2001. Tracing lake trophic history with a chironomid-total phosphorus inference model. *Freshwater Biology* 46, 513-533.
- Brooks, S.J., and Birks, H.J.B., 2001. Chironomid-inferred air temperatures from Lateglacial and Holocene sites in north-west Europe: progress and problems. *Quaternary Science Reviews* 20, 1723-1741.
- Brooks, S.J., Langdon, P.G. and Heiri, O., 2007. The identification and use of Palaeartic Chironomidae larvae in palaeoecology, QRA Technical Guide 10. Quaternary Research Association, London.



## References

- Brundin, L., 1966. Transantarctic relationships and their significance, evidenced by chironomid midges. With a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagylae. *Kungliga Svenska Vetenskapsakademiens Handlingar* 11, 1-472.
- Burney, D.A., 1987. Late Quaternary stratigraphic charcoal records from Madagascar. *Quaternary Research* 28, 274-280.
- Burney, D.A. and Burney, L.P., 2007. Paleoecology and 'inter-situ' restoration on Kaua'i, Hawai'i. *Frontiers in Ecology and the Environment* 5, 483-490.
- Bush, M.B., 2002. Distributional change and conservation on the Andean flank: a palaeoecological perspective. *Global Ecology and Biogeography* 11, 463-473.
- Bush, M.,B. and Gosling, W.D., 2011. Environmental change in the humid tropics and monsoonal regions. In: Matthews, J.A (Ed.), *The handbook of environmental change*. Sage, London.
- Bush, M.B., Hanselman, J.A. and Gosling, W.D., 2010. Nonlinear climate change and Andean feedbacks: an imminent turning point? *Global Change Biology* 16, 3223-3232.
- Bush, M.B., Hanselman, J.A. and Hooghiemstra, H., 2007. Andean montane forests and climate change. In: Flenley, J.R. (Ed.), *Tropical rainforest responses to climatic change*. Springer, Berlin Heidelberg, pp. 33-54.
- Bush, M.B., Hansen, B.C.S., Rodbell, D.T., Seltzer, G.O., Young, K.R., León, B., Abbott, M.B., Silman, M.R. and Gosling, W.D., 2005. A 17,000-year history of Andean climate and vegetation change from Laguna de Chochos, Peru. *Journal of Quaternary Science* 20, 703-714.
- Bush, M.B., Silman, M. and Urrego, D.H., 2004. 48,000 years of climate and forest change in a biodiversity hot spot. *Science* 303, 827-829.
- Bush, M.B., Silman, M.R., McMichael, C. and Saatchi, S., 2008. Fire, climate change and biodiversity in Amazonia: a Late-Holocene perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363, 1795-1802.
- Bush, M.B. and Weng, C., 2006. Introducing a new (freeware) tool for palynology. *Journal of Biogeography* 34, 377-380.

- Byers, A.C., 2000. Contemporary landscape change in the Huascarán National Park and buffer zone. Cordillera Blanca, Peru. Mountain Research and Development 20, 52-63.
- Cárdenas, M.L., Gosling, W.D., Sherlock, S.C., Poole, I., Pennington, R.T. and Mothes, P., 2011. The response of vegetation on the Andean flank in Western Amazonia to Pleistocene climate change. Science 331, 1055-1058.
- Cahill, J.R.A. and Matthysen, E., 2007. Habitat use by two specialist birds in high-Andean *Polylepis* forests. Biological Conservation 140, 62-69.
- Capriles, J.M. and Bedregal, E.F., 2002. The economic, symbolic, and social importance of the "kenua" (*Polylepis* spp.) during prehistoric times in the Andean highlands of Bolivia. Ecotropica 8, 225 - 231.
- Cassard, D., 1999. GIS Andes: A metallogenic GIS of the Andes Cordillera. In: 4th international symposium on Andean geodynamics: extended abstracts. Institut de Recherche pour le Developpement, Paris, pp. 147-150.
- Chen, J., Chen, F., Zhang, E., Brooks, S., Zhou, A. and Zhang, J., 2009. A 1000-year chironomid-based salinity reconstruction from varved sediments of Sugan Lake, Qaidam Basin, arid Northwest China, and its palaeoclimatic significance. Chinese Science Bulletin 54, 3749-3759.
- Chepstow-Lusty, A.J., Bennett, K.D., Fjeldså, J., Kendall, A., Galiano, W. and Herrera, A.T., 1998. Tracing 4,000 years of environmental history in the Cuzco area, Peru, from the pollen record. Mountain Research and Development 18, 159-172.
- Chepstow-Lusty, A.J., Bennett, K.D., Switsur, V.R. and Kendall, A., 1996. 4000 years of human impact and vegetation change in the central Peruvian Andes - with events parallelling the Maya record? Antiquity 70, 824-833.
- Chepstow-Lusty, A.J., Bush, M.B., Frogley, M.R., Baker, P.A., Fritz, S.C. and Aronson, J., 2005. Vegetation and climate change on the Bolivian Altiplano between 108,000 and 18,000 yr ago. Quaternary Research 63, 90 - 98.
- Chepstow-Lusty, A.J., Frogley, M.R., Bauer, B.S., Bush, M.B., and Herrera, A.T., 2003. A Late Holocene record of arid events from the Cuzco region, Peru. Journal of Quaternary Science 18, 491-502.

## References

- Chepstow-Lusty, A.J., Frogley, M.R., Bauer, B.S., Leng, M.J., Boessenkool, K.P., Carcaillet, C., Ali, A.A., and Gioda, A., 2009. Putting the rise of the Inca Empire within a climatic and land management context. *Climate of the Past* 5, 375-388.
- Chepstow-Lusty, A.J., Frogley, M.R., Bauer, B.S., Leng, M.J., Cundy, A.B., Boessenkool, K.P. and Gioda, A., 2007. Evaluating socio-economic change in the Andes using oribatid mite abundances as indicators of domestic animal densities. *Journal of Archaeological Science* 34, 1178-118.
- Chepstow-Lusty, A.J. and Winfield, M., 2000. Inca agroforestry: lessons from the past. *Ambio* 29, 322-328.
- Chiang, J.C.H., 2009. The tropics in paleoclimate. *Annual Review of Earth and Planetary Sciences* 37, 263-297.
- Cierjacks, A., Rühr, N., Wesche, K., and Hensen, I., 2008. Effects of altitude and livestock on the regeneration of two tree line forming *Polylepis* species in Ecuador. *Plant Ecology* 194, 207-221.
- Cincotta, R.P., Wisnewski, J. and Engelman, R., 2000. Human population in the biodiversity hotspots. *Nature* 404, 990-992.
- Clark, J.S., 1988a. Effect of climate change on fire regimes in northwestern Minnesota. *Nature* 334, 233-235.
- Clark, J.S., 1988b. Particle motion and the theory of charcoal analysis: Source area, transport, deposition, and sampling. *Quaternary Research* 30, 67-80.
- Clark, J.S., 1988c. Stratigraphic charcoal analysis on petrographic thin sections: Application to fire history in northwestern Minnesota. *Quaternary Research* 30, 81-91.
- Clark, J.S., Lynch, J., Stocks, B.J. and Golammer, J.G., 1998. Relationships between charcoal particles in air and sediments in west-central Siberia. *The Holocene* 8, 19-29.
- Clark, J.S. and Patterson, W.A., 1997. Background and local charcoal in sediments: scales of fire evidence in the paleorecord. In: Clark, J.S, Cachier, H., Goldammer, J.G. and Stocks, B.J (Eds.), *Sediment records of biomass burning and global change*. Springer, New York, pp. 23-48.

- Clark, J.S. and Royall, P.D., 1995. Particle-size evidence for source areas of charcoal accumulation in Late Holocene sediments of eastern North American lakes. *Quaternary Research* 43, 80-89.
- Colinvaux, P., de Oliveira, P.E. and Moreno, J.E., 1999. Amazon pollen manual and atlas. Harwood Academic, Amsterdam.
- Coltorti, M., Fazio, J.D., Rios, F.P. and Tito, G., 2010. The Nuagapua alluvial fan sequence: Early and Late Holocene human-induced changes in the Bolivian Chaco? *Proceedings of the Geologists' Association* 121, 218-228.
- Correa-Metrio, A., Cabrera, K.R. and Bush, M.B., 2010. Quantifying ecological change through discriminant analysis: a paleoecological example from the Peruvian Amazon. *Journal of Vegetation Science* 21, 695-704.
- Cook, K.H., 2009. South American climate variability and change: remote and regional forcing processes. In: Vimeux, F., Sylvestre, F. and Khodri, M. (Eds.), *Past climate variability in South America and surrounding regions*. Springer, pp. 193-212.
- Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P. and van den Belt, M., 1987. The Value of the World's ecosystem services and natural capital. *Nature* 387, 253-260.
- Craig, H., 1957. Isotopic standards for carbon and oxygen and correction factors for mass spectrometric analysis of carbon dioxide. *Geochemica et Cosmochemica Acta* 12, pp. 133–149.
- Cross, S.L., Baker, P.A., Seltzer, G.O., Fritz, S.C. and Dunbar, R.B., 2000. A new estimate of the Holocene lowstand level of Lake Titicaca, central Andes, and implications for tropical palaeohydrology. *The Holocene* 10, 21-32.
- Cwynar, L.C., 1978. Recent history of fire and vegetation from laminated sediment of Greenloaf Lake, Algonquin Park, Ontario. *Canadian Journal of Botany* 56, 10-21.
- Daily, G.C., 1997. Introduction: what are ecosystem services? In: Daily, G. (Ed.), *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, D.C., pp. 1-10.
- Davies, A.L. and Bunting, M.J., 2010. Applications of palaeoecology in conservation. *The Open Ecology Journal* 3, 54-67.

## References

- Davis, O.K., Kolva, D.K. and Mehringer, P.J., 1977. Pollen analysis of Wildcat Lake, Whitman County, Washington: the last 1000 years. *Northwest Science* 51, 13-30.
- Davis, O.K. and Shafer, D.S., 2006. *Sporormiella* fungal spores, a palynological means of detecting herbivore density. *Palaeogeography, Palaeoclimatology, Palaeoecology* 237, 40-50.
- Dearing, J., 1994. Environmental magnetic susceptibility: using the Bartington MS2 System. Chi Publishing.
- Dearing, J., Battarbee, R., Dikau, R., Larocque, I. and Oldfield, F., 2006. Human–environment interactions: learning from the past. *Regional Environmental Change* 6, 1-16.
- Dejoux, C. and Iltis, A., 1992. Lake Titicaca : a synthesis of limnological knowledge. Kluwer Academic Publishers, Dordrecht.
- De la Barra, N., 2003. Ecological classification of aquatic vegetation of lacustrine systems in Bolivia. *Revista Boliviana De Ecología y Conservación Ambiental* 13, 65-93.
- Dieffenbacher-Krall, A.C., Vandergoes, M.J., Woodward, C.A. and Boothroyd, I.K.G., 2008. Guide to identification and ecology of New Zealand subfossil chironomids found in lake sediment. Climate Change Institute, University of Maine, Orono. (Online: <http://www.climatechange.umaine.edu/Research/facilities/perl/nzguide.html>).
- Dillehay, T.D., 1999. The Late Pleistocene cultures of South America. *Evolutionary Anthropology: Issues, News, and Reviews* 7, 206-216.
- Dillehay, T.D., 2000. The settlement of the Americas: A new prehistory. Basic Books, New York.
- Dillehay, T.D., 2008. Profiles in Pleistocene history. In: Silverman, H. and Isbell, W.H. (Eds.), *The Handbook of South American Archaeology*. Springer, New York, pp. 29-43.
- Donato, M., Massaferro, J. and Brooks, S.J., 2008. Chironomid (Chironomidae: Diptera) checklist from Nahuel Huapi National Park, Patagonia, Argentina. *Revista de la Sociedad Entomológica Argentina* 67, 163-170.
- Edwards, F.W., 1931. Diptera of Patagonia and South Chile. Part II. Fascicle 5. Chironomidae. Trustees of the British Museum, London, pp. 233-331.
- Ellenberg, H., 1958. Wald oder Steppe? Die natürliche Pflanzendecke der Anden Perus. *Umschau*, 645-681.

- Ellenberg, H., 1979. Man's influence on tropical mountain ecosystems in South America: the second Tansley lecture. *Journal of Ecology* 67, 401-416.
- Enache, M.D. and Cumming, B.F., 2006. Tracking recorded fires using charcoal morphology from the sedimentary sequence of Prosser Lake, British Columbia (Canada). *Quaternary Research* 65, 282-292.
- EPICA Community Members., 2004. Eight glacial cycles from an Antarctic ice core. *Nature* 429, 623-628.
- Epler, J.H., 1995. Identification manual for the larval Chironomidae (Diptera) of Florida. Florida Department of Environmental Protection. (Online: <http://www.floridadep.org/labs/cgi-bin/sbio/keys.asp#keys>).
- Epler, J.H., 2001. Identification Manual for the larval Chironomidae (Diptera) of North and South Carolina. A guide to the taxonomy of the midges of the southeastern United States, including Florida. Special Publication SJ2001-SP13. North Carolina Department of Environment and Natural Resources, Raleigh, NC, and St. Johns River Water Management District, Palatka, FL. (Online: <http://www.esb.enr.state.nc.us/BAUwww/Chironomid.htm>).
- Ergueta S, P., and de Morales, C. 1996. Libro Rojo de los Vertebrados de Bolivia. Centro de Datos para la Conservación, La Paz.
- Faegri, K. and Iversen, J., 1989. Textbook of pollen analysis. Blackburn Press, New Jersey.
- Fairbanks, R.G., Mortlock, R.A., Chiu, T.C., Cao, L., Kaplan, A., Guilderson, T.P., Fairbanks, T.W., Bloom, A.L., Grootes, P.M. and Nadeau, M.J., 2005. Radiocarbon calibration curve spanning 0 to 50,000 years BP based on paired  $^{230}\text{Th}/^{234}\text{U}/^{238}\text{U}$  and  $^{14}\text{C}$  dates on pristine corals. *Quaternary Science Reviews* 24, 1781-1796.
- Feeley, K.J., Silman, M.R., Bush, M.B., Farfan, W., Cabrera, K.G., Malhi, Y., Meir, P., Revilla, N.S., Quisiyupanqui, M.N.R. and Saatchi, S., 2011. Upslope migration of Andean trees. *Journal of Biogeography* 38, 783-791.
- Fehse, J., Hofstede, R., Aguirre, N., Paladines, C., Kooijman, A. and Sevink, J., 2002. High altitude tropical secondary forests: a competitive carbon sink? *Forest Ecology and Management* 163, 9-25.
- Fernández, E., 1997. Estudio fitosociológico de los bosques de kewiña (*Polylepis* spp., Rosaceae) en la Cordillera de Cochabamba. *Revista Boliviana De Ecología y Conservacion Ambiental* 2, 49-65.

## References

- Fernández, M., Mercado, M., Arrázola, S., and Martínez, E., 2001. Estructura y composición florística de un fragmento boscoso de *Polylepis bessi*. *Revista Boliviana De Ecología y Conservación Ambiental* 9, 15-27.
- Ferrington, L., 2008. Global diversity of non-biting midges (Chironomidae; Insecta; Diptera) in freshwater. *Hydrobiologia* 595, 447-455.
- Ferreira, R., 1988. Flora y Vegetación del Perú. In: Dourojeanni, M.J. (Ed.), *Gran geografía del Perú. Naturaleza y Hombre*, Tomo 2. Monfer-Juan Mejía Baca, pp. 175.
- Fjeldsø, J., 2002. *Polylepis* forests-vestiges of a vanishing ecosystem in the Andes. *Ecotropica* 8, 111-123.
- Fjeldsø, J., 2007. The relationship between biodiversity and population centres: the high Andes region as an example. *Biodiversity and Conservation* 16, 2739-2751.
- Fjeldsø, J. and Irestedt, M., 2009. Diversification of South American avifauna: patterns and implication for conservation in the Andes. *Annals of the Missouri Botanical Garden* 96, 398-409.
- Fjeldsø, J. and Kessler, M. 1996. Conserving the biological diversity of *Polylepis* woodlands of the highland of Peru and Bolivia: a contribution to sustainable natural resource management in the Andes. NORDECO, Copenhagen.
- Fossa, A.M., Sykes, M.T., Lawesson, J.E. and Gaard, M., 2004. Potential effects of climate change on plant species in the Faeroe Islands. *Global Ecology and Biogeography* 13, 427-437.
- Foster, R.B., Parker III, T.A., Gentry, A.H., Emmons, L.H., Chicchon, A., Schulenberg, T., Rodriguez, L., Lamas, G., Ortega, H., Icochea, J., Wust, W., Romo, M., Castillo, J.A., Phillips, O., Reynel, C., Kratter, A., Donahue, P.K. and Barkley, L.J., 1994. The Tambopata-Candamo Reserved Zone of southeastern Perú: a biological assessment. RAP Working papers 6. Conservation International, Washington D.C.
- Francou, B., Ribstein, P., Wagnon, P., Ramirez, E. and Pouyaud, B., 2005. Glaciers of the Tropical Andes: indicators of the global climate variability. In: Huber, U.M., Bugmann, H.K.M. and Reasoner, M.A. (Eds.), *Global change and mountain regions: a state of knowledge overview*. Springer, Berlin, pp. 197-204.

- Francou, B., Vuille, M., Wagnon, P., Mendoza, J. and Sicart, J.E., 2003. Tropical climate change recorded by a glacier in the central Andes during the last decades of the twentieth century: Chacaltaya, Bolivia, 16°S. *Journal of Geophysical Research* 108, 4154.
- Francus, P., 2005. Image analysis, sediments and paleoenvironments. Kluwer Academic Publishers, Dordrecht.
- Freeman, S., Bishop, P., Bryant, C., Cook, G., Dougans, D., Ertunc, T., Fallick, A., Ganeshram, R., Maden, C., Naysmith, P., Schnabel, C., Scott, M., Summerfield, M. and Xu, S., 2007. The SUERC AMS laboratory after 3 years. *Nuclear Instruments and Methods in Physics Research Section B: Beam Interactions with Materials and Atoms* 259, 66-70.
- Froyd, C.A., and Willis, K.J., 2008. Emerging issues in biodiversity & conservation management: The need for a palaeoecological perspective. *Quaternary Science Reviews* 27, 1723-1732.
- Fritz, S.C. and Saros, J. E., 2006. *Paleolimnology and Paleohydrology*. John Wiley & Sons Ltd.
- Gams, H., 1927. Die Geschichte der Lunzer Seen, Moore und Wfilder. *Internationale revue der gesamten Hydrobiologie und Hydrographie* 18, 305-387.
- García, E., Fernández, M. and Stanton, S. 2010. Dendrochronological investigation of the high Andean tree species *Polylepis besseri* and implications for management and conservation. *Biodiversity and Conservation* 19, 1839-1851.
- Gathorne-Hardy, F.J., Lawson, I.T., Church, M.J., Brooks, S.J., Buckland, P.C., and Edwards, K.J., 2007. The Chironomidae of Grothusvatn, Sandoy, Faroe Islands: climatic and lake-phosphorus reconstructions, and the impact of human settlement. *The Holocene* 17, 1259-1264.
- Gill, J.L., Williams, J.W., Jackson, S.T., Lininger, K.B. and Robinson, G.S., 2009. Pleistocene Megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science* 326, 1100-1103.
- Glew, J.R., Smol, J.P. and Last, W.M., 2001. Sediment Core Collection and Extrusion. In: Last W.M and Smol, J.P. (Eds.), *Tracking Environmental Change Using Lake Sediments. Volume 1: basin analysis, coring and chronological techniques*. Kluwer Academic Publishers, Dordrecht. pp. 73-105.



## References

- Godwin, H. 1956. History of British Flora. Cambridge University Press, Cambridge.
- Goitia, E., Ayala, R., Rossberg, M. and Romero, A.M., 2001. Comunidad bentónica del Rio Rocha en relación a la entrada de poluentes (Cochabamba Boliva). Revista Bolivian de Ecología y Consevacion Ambiental 10, 3-6.
- González, J.A., Gallardo, M.G., Boero, C., Liberman Cruz, M. and Prado, F.E., 2007. Altitudinal and seasonal variation of protective and photosynthetic pigments in leaves of the world's highest elevation trees *Polylepis tarapacana* (Rosaceae). Acta Oecologica 32, 36-41.
- Gosling, W.D. and Bunting, M.J., 2008. A role for palaeoecology in anticipating future change in mountain regions? Palaeogeography, Palaeoclimatology, Palaeoecology 259, 1-5.
- Gosling, W.D., Hanselman, J.A., Knox, C., Valencia, B.G. and Bush, M.B., 2009. Long-term drivers of change in *Polylepis* woodland distribution in the central Andes. Journal of Vegetation Science 20, 1041-1052.
- Gotkowitz, L., 2007. A revolution for our rights: indigenous struggles for land and justice in Bolivia, 1880-1922. Duke University Press, Durham.
- Graf, K.F., 1981., Palynological investigations of two post-glacial peat bogs near the boundary of Bolivia and Peru. Journal of Biogeography 8, 353-368.
- Graf, K.F., 1979. Untersuchungen zur rezenten pollen und sporenflora in der nordlichen Zentralkordillere Boliviens und Versuch einer Auswertung von Profilen aus postglazialen Torfmooren. Habilitationsschrift zur Erlangung der Venia legendi, Philosophischen Fakultät der Universität Zurich. Juris Druck and Verlag, Zurich.
- Graham, A., 2009. The Andes: a geological overview from a biological perspective. Annals of the Missouri Botanical Garden 96, 371-385.
- Gregory-Wodzicki, K.M., 2000. Uplift history of the Central and Northern Andes: A review. Geological Society of America Bulletin 112, 1091-1105.
- Grimm, E.C., Maher Jr, L.J. and Nelson, D.M., 2009. The magnitude of error in conventional bulk-sediment radiocarbon dates from central North America. Quaternary Research 72, 301-308.
- Grosjean, M., 2001. Mid-Holocene climate in the south-central Andes: humid or dry? Science 292, 2391.

- Grosjean, M., Núñez, L., Cartajena, I. and Messerli, B., 1997. Mid-Holocene climate and culture change in the Atacama Desert, northern Chile. *Quaternary Research* 48, 239-246.
- Hanselman, J.A., Bush, M.B., Gosling, W.D., Collins, A., Knox, C., Baker, P.A. and Fritz, S.C., 2011. A 370,000-year record of vegetation and fire history around Lake Titicaca (Bolivia/Peru). *Palaeogeography, Palaeoclimatology, Palaeoecology* (In Press). DOI: 10.1016/j.palaeo.2011.03.002.
- Hanselman, J.A., Gosling, W.D., Paduano, G.M. and Bush, M.B., 2005. Contrasting pollen histories of MIS 5e and the Holocene from Lake Titicaca (Bolivia/Peru). *Journal of Quaternary Science* 20, 663-670.
- Hansen, B.C.S., Wright, H.E.J. and Bradbury, J.P., 1984. Pollen studies in the Junín area, central Peruvian Andes. *Geological Society of America Bulletin* 95, 1454-1465.
- Hastorf, C.A., 2008. The Formative Period in the Titicaca Basin In: Silverman, H. and Isbell, W.H. (Eds.), *The Handbook of South American Archaeology*. Springer, New York, pp. 545-561.
- Heiri, O. and Lotter, A., 2010. How does taxonomic resolution affect chironomid-based temperature reconstruction? *Journal of Paleolimnology* 44, 589-601.
- Heiri, O. and Lotter, A.F., 2001. Effect of low count sums on quantitative environmental reconstructions: an example using subfossil chironomids. *Journal of Paleolimnology* 26, 343-350.
- Heiri, O., Lotter, A.F. and Lemcke, G., 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology* 25, 101-110.
- Hensen, I., 2002. Impacts of anthropogenic activity on the vegetation of *Polylepis* woodlands in the region of Cochabamba, Bolivia. *Ecotropica* 8, 183-203.
- Herbert, T.D. and D'Hondt, S.L., 1990. Precessional climate cyclicity in Late Cretaceous--Early Tertiary marine sediments: a high resolution chronometer of Cretaceous--Tertiary boundary events. *Earth and Planetary Science Letters* 99, 263-275.
- Hertel, D. and Wesche, K., 2008. Tropical moist *Polylepis* stands at the treeline in east Bolivia: the effect of elevation on stand microclimate, above- and below-ground structure, and regeneration. *Trees: Structure and Function* 22, 303-315.

## References

- Higuera, P.E., Peters, M.E., Brubaker, L.B. and Gavin, D.G., 2007. Understanding the origin and analysis of sediment-charcoal records with a simulation model. *Quaternary Science Reviews* 26, 1790-1809.
- Higueras, A., 1996. Prehispanic settlement and land use in Cochabamba, Bolivia. Unpublished Ph.D. thesis. University of Pittsburgh, Pittsburgh.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. and Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25, 1965-1978.
- Hillyer, R., Valencia, B.G., Bush, M.B., Silman, M.R. and Steinitz-Kannan, M., 2009. A 24,700 yr paleolimnological history from the Peruvian Andes. *Quaternary Research* 71, 71-82.
- Hofmann, W., 1988. The significance of chironomid analysis (Insecta: Diptera) for paleolimnological research. *Palaeogeography, Palaeoclimatology, Palaeoecology* 62, 501-509.
- Hofmann, W., 1998. Cladocerans and chironomids as indicators of lake level changes in north temperate lakes. *Journal of Paleolimnology* 19, 55-62.
- Holling, C.S., 1973. Resilience and stability of ecological systems. *Annual Review of Ecological Systems* 4, 1-23.
- Hooghiemstra, H., 1984. Vegetational and climatic history of the high plain of Bogota Colombia: A continuous record of the last 3.5 million Years. Gantner Verlag, Vaduz.
- Hoorn, C., Wesselingh, F. P., ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J., Sanmartín, I., Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P., Jaramillo, C., Riff, D., Negri, F.R., Hooghiemstra, H., Lundberg, J., Stadler, T., Sarkinen, T., Antonelli, A., 2010. Amazonia Through Time: Andean Uplift, Climate Change, Landscape Evolution, and Biodiversity. *Science* 330, 927-931
- Ibisch, P.L., Beck, S.G., Gerkmann, B. and Carretero, A. 2003. Ecoregiones y ecosistemas. In: Ibisch, P.L. and Mérida, G. (Eds.), *Biodiversidad: la riqueza de Bolivia. Estado de conocimiento y conservación*. FAN, Santa Cruz de la Sierra, Bolivia, pp. 47-88.
- Il'yashuk, E.A. and Il'yashuk, B.P., 2004. Analysis of chironomid remains from lake sediments in paleoecological reconstruction. *Water Resources* 31, 203-214.

- Instituto Nacional de Estadística., 2002. Informe del Censo Nacional de Población y Vivienda Bolivia 2001. INE, La Paz.
- IPCC, 2007. Climate Change 2007: The physical science basis (summary for policy makers). Geneva.
- Isbell, W.H., 2008. Wari and Tiwanaku: international identities in the Central Andean Middle Horizon In: Silverman, H. and Isbell, W.H. (Eds.), The Handbook of South American Archaeology. Springer, New York , pp. 731-759.
- Jameson, J.S. and Ramsay, P.M., 2007. Changes in high-altitude *Polylepis* forest cover and quality in the Cordillera de Vilcanota, Perú, 1956-2005. Biological Conservation 138, 38-46.
- Jankovská, V. and Komárek, J., 2000. Indicative value of *Pediastrum* and other coccal green algae in palaeoecology. Folia Geobotanica 35, 59-82.
- Janusek, J.W., 2008. Ancient Tiwanaku (Case studies in early societies) Cambridge University Press, New York.
- Jarvis, A., Touval, J.L., Schmitz, M.C., Sotomayor, L. and Hyman, G.G., 2010. Assessment of threats to ecosystems in South America. Journal for Nature Conservation 18, 180-188.
- Jensen, K., Lynch, E.A., Calcote, R. and Hotchkiss, S.C., 2007. Interpretation of charcoal morphotypes in sediments from Ferry Lake, Wisconsin, USA: do different plant fuel sources produce distinctive charcoal morphotypes? The Holocene 17, 907-915.
- Johnson, M.G., Kelso, J.R.M., McNeil, O.C. and Morton, W.B., 1990. Fossil midge associations and historical status of fish acidified lakes. Journal of Paleolimnology 62, 501-509.
- Johnsen, S.J., Dahl-Jensen, D., Gundestrup, N., Steffensen, J.P. and Clausen, H.B., 2001. Oxygen isotope and palaeotemperature records from six Greenland ice-core stations: Camp Century, Dye-3, GRIP, GISP2, Renland and NorthGRIP. Journal of Quaternary Science 16, 299-307.
- Jouzel, J., Genthon, C., Lorius, C., Petit, J.R. and Barkov, N.I., 1987. Vostok ice core: a continuous isotope temperature record over the last climatic cycle (160,000 years). Nature 329, 403-408.
- Juggins, S., 2002. WinTran (V.1.4). University of Newcastle, Newcastle upon Tyne.

- Juggins, S., 2003. C2 data analysis (V.1.4Beta). University of Newcastle, Newcastle upon Tyne.
- Kansanen, P.H., 1985. Assessment of pollution history from recent sediments in Lake Vanajavesi, southern Finland. II. Changes in the Chironomidae, Chaoboridae and Ceratopogonidae (Diptera) fauna. *Annales Zoologici Fennici* 22, 13-55.
- Kennan, L., Lamb, S.H. and Hoke, L., 1997. High-altitude palaeosurfaces in the Bolivian Andes: evidence for late Cenozoic surface uplift. In: Widdowson, M. (Ed.), *Palaeosurfaces: recognition, reconstruction and palaeoenvironmental interpretation*. Geological Society Special Publication No. 120, pp. 307-323.
- Kessler, M., 1995. Present and potential distribution of *Polylepis* (Rosaceae) forests in Bolivia. In: Churchill, S.P., Balslev, H., Forero, E. and Luteyn, J.L. Eds.), *Biodiversity and conservation of neotropical montane forests*. New York Botanical Garden, New York, pp. 281-294.
- Kessler, M., 1999. Plant species richness and endemism during natural landslide succession in a perhumid montane forest in the Bolivian Andes. *Ecotropica* 5, 123-136.
- Kessler, M., 2002a. The "*Polylepis* Problem": where do we stand? *Ecotropica* 8, 97-110.
- Kessler, M., 2002b. Range size and its ecological correlates among the pteridophytes of Carrasco National Park, Bolivia. *Global Ecology and Biogeography* 11, 89-102.
- Kessler, M. and Schmidt-Lebuhn, A.N., 2006. Taxonomical and distributional notes on *Polylepis* (Rosaceae). *Organisms, Diversity & Evolution* 6, 67-69.
- Kessler, C.A. and Stroosnijder, L., 2006. Land degradation assessment by farmers in Bolivian mountain valleys. *Land Degradation & Development* 17, 235-248.
- Killeen, T.J., Douglas, M., Consiglio, T., Jørgensen, P.M. and Mejia, J., 2007. Dry spots and wet spots in the Andean hotspot. *Journal of Biogeography* 34, 1357-1373.
- Klanderud, K. and Birks, H.J.B., 2003. Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *The Holocene* 13, 1-6.
- Kohshima, S., 1984. A novel cold-tolerant insect found in a Himalayan glacier. *Nature* 310, 225-227.
- Kolata, A.L., 1993. *Tiwanaku: portrait of an Andean civilization*. Blackwell, Cambridge.

- Kolata, A.L., 1996. Tiwanaku and its hinterland: archaeology and paleoecology of an Andean civilization. Volume 1: Argroecology. Smithsonian Institution Press, Washington D.C.
- Komárek, J. and Jankovská, V., 2001. Review of the green algal genus *Pediastrum*; implication for pollen analytical research. *Bibliotheca Phycologia* 108, 1–125.
- Körner, C. and Paulsen, J., 2004. A world-wide study of high altitude treeline temperatures. *Journal of Biogeography* 31, 713-732.
- Kull, C., Imhof, S., Grosjean, M., Zech, R. and Veit, H., 2008. Late Pleistocene glaciation in the Central Andes: temperature versus humidity control. A case study from the eastern Bolivian Andes (17°S) and regional synthesis. *Global and Planetary Change* 60, 148-164.
- Lamb, S. and Hoke, L., 1997. Origin of the high plateau in the Central Andes, Bolivia, South America. *Tectonics* 16, 623-649.
- Lamoureux, S.F. and Bollmann, J., 2005. Image acquisition. In: Francus, P. (Ed.), *Developments in paleoenvironmental research 7: image analysis, sediments and paleoenvironments*. Kluwer Academic Publishers, Dordrecht, pp. 11-34.
- Lang, B., Bedford, A., Brooks, S.J., Jones, R.T., Richardson, N., Birks, H.J.B. and Marshall, J.D., 2010. Early-Holocene temperature variability inferred from chironomid assemblages at Hawes Water, northwest England. *The Holocene* 20, 943-954.
- Larocque, I., 2001. How many chironomid head capsules are enough? A statistical approach to determine sample size for palaeoclimatic reconstructions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 172, 133-142.
- Larson, B., 1998. Cochabamba, 1550-1900: Colonialism and agrarian transformation in Bolivia. Duke University Press, Durham.
- Lavallée, D., 2000. The first South Americans: the peopling of a continent from the earliest evidence to high culture. University of Utah Press, Salt Lake City.
- Leduc, G., Vidal, L., Tachikawa, K. and Bard, E., 2009. ITCZ rather than ENSO signature for abrupt climate changes across the tropical Pacific? *Quaternary Research* 72, 123-131.
- Lenoir, J., Gegout, J.C., Marquet, P.A., de Ruffray, P. and Brisse, H., 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320, 1768-1771.

## References

- Line, J.M. and Birks, H.J.B., 1996. BSTICK (V.1.0). Unpublished computer program. Botanical Institute, University of Bergen.
- Livingstone, D.A., 1955. A lightweight piston sampler for lake deposits. *Ecology* 36, 137-139.
- Lone, M.B.L. and Lone, D.E.L., 1987. The Inka State in the southern highlands: state administrative and production enclaves. *Ethnohistory* 34, 47-62.
- Lotter, A.F. and Juggins, S., 1991. POLPROF, TRAN and ZONE: programs for plotting, editing and zoning pollen and diatom data. INQUA-Subcommission for the study of the Holocene: Working group on data-handling methods 6, 4-6.
- Lowe, J.J. and Walker, M.J.C., 1997. Reconstructing Quaternary environments. Pearson Prentice Hall, Harlow.
- Lynch, T.F., 1983. Camelid pastoralism and the emergence of Tiwanaku civilization in the south-central Andes. *World Archaeology* 15, 1-14.
- Lynch, T.F., 1990. Quaternary climate, environment, and the human occupation of the south-central Andes. *Geoarchaeology* 5, 199-228.
- Lynch-Stieglitz, J., 2004. Hemispheric asynchrony of abrupt climate change. *Science* 304, 1919-1920.
- Lytle, D.E. and Wahl, E.R., 2005. Palaeoenvironmental reconstructions using the modern analogue technique: the effects of sample size and decision rules. *The Holocene* 15, 554-566.
- MacDonald, G.M., 1993. Fossil pollen analysis and the reconstruction of plant invasions. In: Begon, A. and Fitter, A.H. (Eds.), *Advances in Ecological Research*. Volume 24. Academic Press Limited, London, pp. 67-110.
- Macek, P., Mackov, J. and de Bello, F., 2009. Morphological and ecophysiological traits shaping altitudinal distribution of three *Polylepis* treeline species in the dry Tropical Andes. *Acta Oecologica* 35, 778-785.
- Malcolm, J.R., Liu, C., Neilson, R.P., Hansen, L. and Hannah, L., 2006. Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology* 20, 538-548.
- Marris, E., 2011. The end of the wild. *Nature* 469, 150-152.

- Mamani, M., Wörner, G. and Sempere, T., 2010. Geochemical variations in igneous rocks of the Central Andean orocline (13°S to 18°S): Tracing crustal thickening and magma generation through time and space. *Geological Society of America Bulletin* 122, 162-182.
- Marchant, R., Almeida, L., Behling, H., Berrio, J.C., Bush, M.B., Cleef, A., Duivenvoorden, J., Kappelle, M., De Oliveira, P., Teixeira de Oliveira-Filho, A., Lozano-Garcia, S., Hooghiemstra, H., Ledru, M.P., Ludlow-Wiechers, B., Markgraf, V., Mancini, V., Paez, M., Prieto, A., Rangel, O. and Salgado-Labouriau, M.L., 2002. Distribution and ecology of parent taxa of pollen lodged within the Latin American Pollen Database. *Review of Palaeobotany and Palynology* 121, 1-75.
- Martin, R., Mildenhall, D.C., Browne, P.R.L. and Rodgers, K.A., 2000. The age and significance of in-situ sinter at the Te Kopia thermal area, Taupo Volcanic Zone, New Zealand. *Geothermics* 29, 367-375.
- Massaferro, J.I., Ashworth, A., Brooks, S.J. and Rabassa, J., 2008. Quaternary fossil insects from Patagonia. In: Rabassa, J. (Ed.), *Developments in Quaternary Science. Volume 11: The Late Cenozoic of Patagonia and Tierra del Fuego*. Elsevier, pp. 393-410.
- Massaferro, J.I., Brooks, S.J. and Haberle, S.G., 2005. The dynamics of chironomid assemblages and vegetation during the Late Quaternary at Laguna Facil, Chonos Archipelago, southern Chile. *Quaternary Science Reviews* 24, 2510-2522.
- Massaferro, J.I. and Brooks, S.J. 2002. Response of chironomids to Late Quaternary environmental change in the Taitao Peninsula, southern Chile. *Journal of Quaternary Science* 17, 101-111.
- Massaferro, J.I., Moreno, P.I., Denton, G.H., Vandergoes, M. and Dieffenbacher-Krall, A., 2009. Chironomid and pollen evidence for climate fluctuations during the Last Glacial Termination in NW Patagonia. *Quaternary Science Reviews* 28, 517-525.
- McCormac, F.G., Hogg, A.G., Blackwell, P.G., Buck, C.E., Higham, T.F.G. and Reimer, P.J., 2004. SHCal04 Southern Hemisphere Calibration 0 - 11.0 cal kyr BP. *Radiocarbon* 46, 1087-1092.
- McCune, B. and Mefford, M.J., (2006). *PC-ORD. Multivariate Analysis of Ecological Data (V.5)*. MjM Software, Gleneden Beach, Oregon.



## References

- McElhinny, M.W., 1973. Palaeomagnetism and plate tectonics. Cambridge University Press, Cambridge.
- McMillan, K., 2008. An inexpensive system for continuous lake core photography. *Journal of Paleolimnology* 40, 1179-1184.
- McQuarrie, N., 2002. The kinematic history of the central Andean fold-thrust belt, Bolivia: implications for building a high plateau. *Geological Society of America Bulletin* 114, 950-963.
- Meyers, P.A. and Teranes, J.L., 2001. Sediment organic matter. In: Last, W.M. and Smol, J.P (Eds.), *Tracking Environmental Change Using Lake Sediments*. Kluwer Academic Publishers, Dordrecht, pp. 239-269.
- Miehe, G. and Miehe, S., 1994. Zur oberen Waldgrenze in tropischen Gebirgen. *Phytocoenologia* 24, 53-110.
- Miehe, G. Miehe, S. Vogel, J. Co, S. and Duo, L., 2007. Highest treeline in the northern hemisphere found in southern Tibet. *Mountain Research and Development* 27, 169-173.
- Mittermeier, R.A., Gil, P.R., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J. and da Fonseca, G.A.B., 2004. Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions. Cemex, Mexico City.
- Mix, A.C., Bard, E. and Schneider, R., 2001. Environmental processes of the ice age: land, oceans, glaciers (EPILOG). *Quaternary Science Reviews* 20, 627-657.
- Molina, J.A., Navarro, G., De la Barra, N. and Lumbreras, A., 2007. Andean aquatic vegetation in central Bolivia. *Phytocoenologia* 37, 753-768.
- Mondini, M., 2002. Carnivore taphonomy and the early human occupations in the Andes. *Journal of Archaeological Science* 29, 791-801.
- Montes de Oca, I., 2002. *Geografía y recursos naturales de Bolivia*. La Paz.
- Montes de Oca, I., 2005. *Enciclopedia geográfica de Bolivia*. Editora Atenea S.R.L., La Paz.
- Montgomery, D.R., Balco, G. and Willett, S.D., 2001. Climate, tectonics, and the morphology of the Andes. *Geology* 29, 579-582.
- Moore, P.D., Webb, J.A. and Collinson, M.E., 1991. *Pollen analysis*. Blackwell Scientific, London.

- Mosblech, N.A.S., Bush, M.B. and van Woesik, R., 2011. On metapopulations and microrefugia: palaeoecological insights. *Journal of Biogeography* 38, 419-429.
- Mourguiart, P. and Ledru, M.P., 2003. Last Glacial Maximum in an Andean cloud forest environment (Eastern Cordillera, Bolivia). *Geology* 31, 195-198.
- Moy, C.M., Seltzer, G.O., Rodbell, D.T. and Anderson, D.M., 2002. Variability of El Niño/Southern Oscillation activity at millennial timescales during the Holocene epoch. *Nature* 420, 162-165.
- Murray, B.P., Horton, B.K., Matos, R. and Heizler, M.T., 2010. Oligocene-Miocene basin evolution in the northern Altiplano, Bolivia: Implications for evolution of the central Andean backthrust belt and high plateau. *Geological Society of America Bulletin* 122, 1443-1462.
- Munsell Soil Color Charts., 2000. Munsell Soil Color Charts, Revised Washable Edition. New Windsor, New York.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. and Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853-858.
- Navarro, G. and Ferreira, W., 2007. Mapa de vegetación de Bolivia. CD-ROM interactivo. The Nature Conservancy & Rumbol.
- Navarro, G. and Maldonado, M., 2002. Geografía ecológica de Bolivia: vegetación y ambientes acuáticos. Centro de Ecología Simón I. Patino, Santa Cruz.
- Navarro, G., Molina, J. A. and De la Barra, N., 2005. Classification of the high-Andean *Polylepis* forests in Bolivia. *Plant Ecology* 176, 113 -130.
- Nederbragt, A.J and Thurow, J.W., 2005. Digital sediment colour analysis as a method to obtain high resolution climate proxy records. In: Francus, P. (Ed.), *Developments in paleoenvironmental research 7: image analysis, sediments and paleoenvironments*. Kluwer Academic Publishers, Dordrecht, pp. 105-124.
- Nederbragt, A.J., Dunbar, R.B., Osborn, A.T., Palmer, A., Thurow, J.W. and Wagner, T. 2006. Sediment colour analysis from digital images and correlation with sediment composition. *Geological Society, London, Special Publications* 267, 113-128.
- Nogues-Bravo, D., Araujo, M.B., Romdal, T. and Rahbek, C., 2008. Scale effects and human impact on the elevational species richness gradients. *Nature* 453, 216-219.

- Nowaczyk, N.R., 2001. Logging of magnetic susceptibility. In: Last, W.M. and Smol, J.P. (Eds.), *Tracking environmental change using lake sediments: Volume 1: basin analysis, coring and chronological techniques* Kluwer Academic Publishers, Dordrecht, pp. 155-170.
- Nyman, M., 2007. "Distribution of non-biting midges (Diptera, Chironomidae) in subarctic lakes of Finnish Lapland: applications in lake classification and palaeolimnology." University of Helsinki.
- Nyman, M., Korhola, A. and Brooks, S.J., 2005. The distribution and diversity of Chironomidae (Insecta: Diptera) in western Finnish Lapland, with special emphasis on shallow lakes. *Global Ecology and Biogeography* 14, 137-153.
- Ólafsson, E., Carlström, S. and Ndaro, S.G.M., 2000. Meiobenthos of hypersaline tropical mangrove sediment in relation to spring tide inundation. *Hydrobiologia* 426, 57-64.
- Oldfield, F., 1978. Lakes and their drainage basins as units of sediment-based ecological study. *Progress in Physical Geography* 1, 406-504.
- Oldfield, F., 1991. Environmental magnetism: personal perspective. *Quaternary Science Reviews* 10, 73-85.
- Oller, C.A., 2001. Macroinvertebrados bentónicos y metales pesados en el Río Pilcomayo (Tarija). Unpublished Ph.D. thesis. University of San Simón, Cochabamba.
- Olson, D.M., Dinerstein, E., Hedao, P., Walters, S., Allnutt, P., Loucks, C., Kura, Y., Kassem, K., Webster, A., and Bookbinder, M., 2000. Terrestrial ecoregions of the Neotropical realm. Conservation Science Program, WWF-US, Washington D.C.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. and Kassem, K.R., 2001. Terrestrial ecoregions of the World: a new map of life on Earth. *BioScience* 51, 933-938.
- Ørbæk, J.B., Tombre, I., and Kallenborn, R., 2004. Challenges in arctic-alpine environmental research. *Arctic, Antarctic, and Alpine Research* 36, 281-283.
- Ortuño, T., Ledru, M.P., Cheddadi, R., Kuentz, A., Favier, C. and Beck, S., 2011. Modern pollen rain, vegetation and climate in Bolivian ecoregions. *Review of Palaeobotany and Palynology* 165, 61-74.

## References

- Paduano, G.M., Bush, M.B., Baker, P.A., Fritz, S.C. and Seltzer, G.O., 2003. A vegetation and fire history of Lake Titicaca since the Last Glacial Maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology* 194, 259-279.
- Papworth, S.K., Rist, J., Coad, L. and Milner-Gulland, E.J. 2009. Evidence for shifting baseline syndrome in conservation. *Conservation Letters* 2, 93-100.
- ParksWatch., 1996. Center for Tropical Conservation, Duke University Durham.
- Patterson, W.A., Edwards, K.J. and Maguire, D.J., 1987. Microscopic charcoal as a fossil indicator of fire. *Quaternary Science Reviews* 6, 3-23.
- Pauly, D., 1995. Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution* 10, 430-430.
- Payne, R. and Mitchell, E., 2009. How many is enough? Determining optimal count totals for ecological and palaeoecological studies of testate amoebae. *Journal of Paleolimnology* 42, 483-495.
- Philander, S.G.H., 1990. *El Niño, La Niña, and the Southern Oscillation*. Elsevier, New York.
- Pinder, L.C.V., 1986. Biology of freshwater Chironomidae. *Annual Review of Entomology* 31, 1-23.
- Porinchu, D.F., MacDonald, G.M., Bloom, A.M. and Moser, K.A., 2003. Late Pleistocene and early Holocene climate and limnological changes in the Sierra Nevada, California, USA inferred from midges (Insecta: Diptera: Chironomidae). *Palaeogeography, Palaeoclimatology, Palaeoecology* 198, 403-422.
- Power, M., Marlon, J., Ortiz, N., Bartlein, P., Harrison, S., Mayle, F., Ballouche, A., Bradshaw, R., Carcaillet, C., Cordova, C., Mooney, S., Moreno, P., Prentice, I., Thonicke, K., Tinner, W., Whitlock, C., Zhang, Y., Zhao, Y., Ali, A., Anderson, R., Beer, R., Behling, H., Briles, C., Brown, K., Brunelle, A., Bush, M., Camill, P., Chu, G., Clark, J., Colombaroli, D., Connor, S., Daniau, A. L., Daniels, M., Dodson, J., Doughty, E., Edwards, M., Finsinger, W., Foster, D., Frechette, J., Gaillard, M. J., Gavin, D., Gobet, E., Haberle, S., Hallett, D., Higuera, P., Hope, G., Horn, S., Inoue, J., Kaltenrieder, P., Kennedy, L., Kong, Z., Larsen, C., Long, C., Lynch, J., Lynch, E., McGlone, M., Meeks, S., Mensing, S., Meyer, G., Minckley, T., Mohr, J., Nelson, D., New, J., Newnham, R., Noti, R., Oswald, W., Pierce, J., Richard, P., Rowe, C., Sanchez Goñi, M., Shuman, B., Takahara, H., Toney, J., Turney, C., Urrego-Sanchez, D., Umbanhowar, C., Vandergoes, M., Vanniére, B., Vescovi, E., Walsh, M., Wang,

- X., Williams, N., Wilmschurst, J. and Zhang, J., 2008. Changes in fire regimes since the Last Glacial Maximum: an assessment based on a global synthesis and analysis of charcoal data. *Climate Dynamics* 30, 887-907.
- Purcell, J. and Brelsford, A., 2004. Reassessing the causes of decline of *Polylepis*, a tropical subalpine forest. *Ecotropica* 10, 155-158.
- Quinlan, R. and Smol, J.P., 2001. Chironomid-based inference models for estimating end-of-summer hypolimnetic oxygen from south-central Ontario shield lakes. *Freshwater Biology* 46, 1529–1551.
- Rabatel, A., Francou, B., Jomelli, V., Naveau, P. and Grancher, D., 2008. A chronology of the Little Ice Age in the Tropical Andes of Bolivia (16°S) and its implications for climate reconstruction. *Quaternary Research* 70, 198-212.
- Raper, D. and Bush, M.B., 2009. A test of *Sporormiella* representation as a predictor of megaherbivore presence and abundance. *Quaternary Research* 71, 490-496.
- Rasband, W.S., 1997-2009. ImageJ, U. S. National Institutes of Health, Bethesda Maryland. (Online: <http://rsb.info.nih.gov/ij/>).
- Rasmussen, S.O., Andersen, K.K., Svensson, A.M., Steffensen, J.P., Vinther, B.M., Clausen, H.B., Siggaard-Andersen, M.L., Johnsen, S.J., Larsen, L.B., Dahl-Jensen, D., Bigler, M., Röthlisberger, R., Fischer, H., Goto-Azuma, K., Hansson, M.E. and Ruth, U., 2006. A new Greenland ice core chronology for the last glacial termination. *Journal of Geophysical Research* 111. (Online) DOI:10.1029/2005JD006079.
- Reese, C.A., 2003. Pollen dispersal and deposition in the high-central Andes, South America. Unpublished Ph.D. thesis. Louisiana State University.
- Reese, C.A. and Liu, K.B., 2005. A modern pollen rain study from the central Andes region of South America. *Journal of Biogeography* 32, 709-718.
- Rein, B., Lückge, A., Reinhardt, L., Sirocko, F., Wolf, A. and Dullo, W.C., 2005. El Niño variability off Peru during the last 20,000 years. *Paleoceanography* 20. (Online) DOI: 10.1029/2004PA001099.
- Renison, D., Cingolani, A.M., Suarez, R., Menoyo, E., Coutsiars, C., Sobral, A., and Hensen, I., 2005. The restoration of degraded mountain woodlands: effects of seed provenance and microsite characteristics on *Polylepis australis* seedling survival and growth in central Argentina. *Restoration Ecology* 13, 129-137.

## References

- Renison, D., Hensen, I. and Cingolani, A.M., 2004. Anthropogenic soil degradation affects seed viability in *Polylepis australis* mountain forests of central Argentina. *Forest Ecology and Management* 196, 327-333.
- Renison, D., Hensen, I., Suarez, R. and Cingolani, A.M., 2006. Cover and growth habit of *Polylepis* woodlands and shrublands in the mountains of central Argentina: human or environmental influence? *Journal of Biogeography* 33, 876-887.
- Renison, D., Hensen, I., Suarez, R., Cingolani, A.M., Marcora, P. and Giorgis, M.A., 2010. Soil conservation in *Polylepis* mountain forests of Central Argentina: Is livestock reducing our natural capital? *Austral Ecology* 35, 435-443.
- Rieradevall, M. and Brooks, S.J., 2001. An identification guide to subfossil Tanypodinae larvae (Insecta: Diptera: Chironomidae) based on cephalic setation. *Journal of Paleolimnology* 25, 81-99.
- Ritter, N.P., 2000. Biodiversity and phytogeography of Bolivia's wetland flora. Unpublished Ph.D. thesis, University of New Hampshire.
- Ritter, N.P. and Crow, G.E., 1998. *Myriophyllum quitense* Kunth (Haloragaceae) in Bolivia: a terrestrial growth-form with bisexual flowers. *Aquatic Botany* 60, 389-395.
- Roback, S.S. and Coffman, W.P., 1983. Results of the Catherwood Bolivian-Peruvian Altiplano Expedition Part II. Aquatic Diptera including montane Diamesinae and Orthocladiinae (Chironomidae) from Venezuela. *Proceedings of the Academy of Natural Sciences of Philadelphia* 135, 9-79.
- Rogerson, M., Weaver, P.P.E., Rohling, E.J., Lourens, L.J., Murray, J.W. and Hayes, A., 2006. Colour logging as a tool in high-resolution palaeoceanography. *Geological Society, London, Special Publications* 267, 99-112.
- Roosevelt, A.C., da Costa, M.L., Machado, C.L., Michab, M., Mercier, N., Valladas, H., Feathers, J., Barnett, W., da Silveira, M.I., Henderson, A., Sliva, J., Chernoff, B., Reese, D.S., Holman, J.A., Toth, N. and Schick, K., 1996. Paleoindian cave dwellers in the Amazon: The peopling of the Americas. *Science* 272, 373-384.
- Roubik, D.W. and Moreno, E., 1991. Pollen and spores of Barro Colorado Island. Missouri Botanical Garden.
- Ruse, L.P., 2010. Classification of nutrient impact on lakes using the chironomid pupal exuvial technique. *Ecological Indicators* 10, 594-601.

- Saarinen, T. and Petterson, G., 2001. Image analysis techniques. In: Last, W.M. and Smol, J.P. (Eds.), Tracking environmental changes using lake sediments. Volume 2: physical and geochemical methods. Kluwer Academic Publishers, Dordrecht, pp. 23–39.
- Saavedra, C., 2005. Estimating spatial patterns of soil erosion and deposition in the Andean region using geo-information techniques: A case study in Cochabamba, Bolivia. Unpublished Ph.D. thesis. Wageningen University, Wageningen.
- Sage, C., 1984. Intensification of commodity relations: agricultural specialization and differentiation in the Cochabamba Serranía, Bolivia. Bulletin of Latin American Research 3, 81-97.
- Salgado-Labouriau, M.L., Schubert, C. and Valastro Jr, S., 1977. Paleoecologic analysis of a Late-Quaternary terrace from Mucubaji, Venezuelan Andes. Journal of Biogeography 4, 313-325.
- Salazar, N.E., 2000. Dinámica de la macrofauna asociada a las macrófitas flotantes de la Laguna Alalay (Cochabamba). Unpublished Ph.D. thesis. University of San Simón, Cochabamba.
- Salinas, G., Marin, R.C.H., Fossati, O. and Wasson, J.G., 1999. Efecto de las materia en suspensión sobre los invertebrados bentónicos de los ríos de aguas claras en los Yungas de Bolivia. Revista Boliviana de Ecología y Conservación Ambiental 6, 183-189.
- Sánchez, W.C., 2008. Inkas, “Flecheros” y Mitmaquna. Cambio social y paisajes culturales en los Valles y en los Yungas de Inkachaca/Paracti y Tablas Monte. (Cochabamba-Bolivia, siglos XV-XVI). Unpublished Ph.D. thesis. Uppsala University / University San Simón.
- Sandgren, P. and Snowball, I., 2001. Application of mineral magnetic techniques to paleolimnology. In: Last, W.M. and Smol, J.P. (Eds.), Tracking environmental changes using lake sediments. Volume 2: physical and geochemical methods. Kluwer Academic Publishers, Dordrecht, pp. 217–237.
- Sandweiss, D.H. and Richardson III, J.B., 2008. Central Andean environments. In: (H. Silverman, H. and Isbell, W.H. (Eds.), The handbook of South American archaeology. Springer, New York, pp. 93-104.

## References

- Sandweiss, D.H., Richardson III, J.B., Reitz, E.J., Rollins, H.B. and Maasch, K.A., 1996. Geoarchaeological evidence from Peru for a 5000 years B.P. onset of El Niño. *Science* 273, 1531-1533.
- Sarmiento, L., Llambí, L.D., Escalona, A. and Marquez, N., 2003. Vegetation patterns, regeneration rates and divergence in an old-field succession of the high tropical Andes. *Plant Ecology* 166, 145-156.
- Schakau, B., 1991. Stratigraphy of the fossil Chironomidae (Diptera) from Lake Grasmere, South Island, New Zealand, during the last 6000 years. *Hydrobiologia* 214, 213-221.
- Schumacher, B.A. 2002. Methods for the determination of total organic carbon (TOC) in soils and sediments. United States Environmental Protection Agency, Office of Research and Development, Las Vegas.
- Sharifi, M.A., van den Toorn, W., Rico, A. and Emmanuel, M., 2002. Application of GIS and multicriteria evaluation in locating sustainable boundary between the tunari National Park and Cochabamba City (Bolivia). *Journal of Multi-Criteria Decision Analysis* 11, 151-164.
- Shuman, B., 2003. Controls on loss-on-ignition variation in cores from two shallow lakes in the north-eastern United States. *Journal of Paleolimnology* 30, 371-385.
- Sillar, B., 2000. Dung by preference: The choice of fuel as an example of how Andean pottery production is embedded within wider technical, social and economic practices. *Archaeometry* 42, 43-60.
- Silverman, H. and Isbell, W.H., 2008. *The Handbook of South American Archaeology*. Springer, New York.
- Simpson, B.B., 1979. A revision of the genus *Polylepis* (Rosaceae: Sanguisorbeae). *Smithsonian Contributions to Botany* 43, 1-62.
- Smit, A., 1978. Pollen morphology of *Polylepis* Boyacensis Cuatrecasas, *Acaena* Cylindristachya Ruiz et Pavon and *Acaena* Elongatata L. (Rosaceae) and its application to fossil material. *Review of Palaeobotany and Palynology* 25, 393 - 398.
- Smith, J.A. and Rodbell, D.T., 2010. Cross-cutting moraines reveal evidence for North Atlantic influence on glaciers in the Tropical Andes. *Journal of Quaternary Science* 25, 243-248.



- Spies, M. and Reiss, F., 1996. Catalogue and bibliography of Neotropical and Mexican Chironomidae (Insecta, Diptera). Spixiana Supplement 22, 61-119.
- Stattersfield, A.J., Crosby, M.J., Long, A.J and Wege, D.C., 1998. Endemic bird areas of the World: priorities for biodiversity conservation. Birdlife Conservation Series 7. Birdlife International, Cambridge.
- Stuiver, M. and Reimer, P.J., 1993. Extended <sup>14</sup>C database and revised CALIB radiocarbon calibration program. Radiocarbon 35, 215-230.
- Stuiver, M. Reimer, P.J. and Reimer, R.W., 2005. CALIB Radiocarbon Calibration (V.5.0).
- Stuiver, M. and Reimer, P.J., 2010. CALIB Radiocarbon Calibration Program (V.6.0.1).
- Sylvestre, F., 2009. Moisture Pattern During the Last Glacial Maximum in South America. In: Vimeux, F., Sylvestre, F. and Khodri, M. (Eds.), Past climate variability in South America and surrounding regions. Springer, pp. 3-27.
- Sylvestre, F., Servant, M., Servant-Vildary, S., Causse, C., Fournier, M. and Ybert, J.P., 1999. Lake Level chronology on the southern Bolivian Altiplano (18–23°S) during Late-glacial time and the early Holocene. Quaternary International 51, 54-66.
- Tawackoli, S., Jacobshagen, V., Wemmer, K. and Andriessen, P.A.M., 1996. The Eastern Cordillera of southern Bolivia: a key region to the Andean backarc uplift and deformation history. In: Third International Symposium on Andean Geodynamics (ISAG). ORSTOM, St. Malo, France, pp. 505-508.
- Teich, I., Cingolani, A.M., Renison, D., Hensen, I. and Giorgis, M.A., 2005. Do domestic herbivores retard *Polylepis australis* Bitt. woodland recovery in the mountains of Córdoba, Argentina? Forest Ecology and Management 219, 229-241.
- Thompson, L.G., Davis, M.E., Mosley-Thompson, E., Sowers, T.A., Henderson, K.A., Zagorodnov, V.S., Lin, P.N., Mikhalev, V.N., Campen, R.K., Bolzan, J.F., Cole-Dai, J. and Francou, B., 1998. A 25,000 year tropical climate history from Bolivian ice cores. Science 282, 1858-1864.
- Thompson, L.G., Mosley-Thompson, E., Bolzan, J.F. and Koci, B.R., 1985. A 1500 year record of tropical precipitation in ice cores from the Quelccaya Ice Cap, Peru. Science 229, 971-973.
- Thompson, L.G., Mosley-Thompson, E. and Henderson, K.A., 2000. Ice-core palaeoclimate records in tropical South America since the Last Glacial Maximum. Journal of Quaternary Science 15, 377-394.

## References

- Thompson, R., Battarbee, R.W., O'Sullivan, P.E. and Oldfield, F., 1975. Magnetic susceptibility of lake sediments. *Limnology and Oceanography* 20, 687-698.
- Thompson, R. and Oldfield, F., 1986. *Environmental magnetism*. George Allen and Unwin, London.
- Tiberti, R., Tartari, G.A. and Marchetto, A., 2010. Geomorphology and hydrochemistry of 12 Alpine lakes in the Gran Paradiso National Park, Italy *Journal of Limnology* 69, 242-256.
- Tinner, W., Hofstetter, S., Zeugin, F., Conedera, M., Wohlgemuth, T., Zimmermann, L. and Zweifel, R., 2006. Long-distance transport of macroscopic charcoal by an intensive crown fire in the Swiss Alps: implications for fire history reconstruction. *The Holocene* 16, 287-292.
- Traverse, A. 1988. *Paleopalynology*. Unwin Hyman, Boston.
- Tutiempo Network., 2010. *Historical Weather: Cochabamba, Bolivia*. Tutiempo Network SL, Madrid. (Online: <http://TuTiempo.net>).
- UNESCO., 1980. *Vegetation map of South America: Map 1:5,000,000*. Institut de la carte internationale de tapis vegetal, Toulouse, France.
- Urrego, D.H., Bush, M.B. and Silman, M.R., 2010. A long history of cloud and forest migration from Lake Consuelo, Peru. *Quaternary Research* 73, 364-373.
- Urrego, D.H., Bush, M.B., Silman, M.R., Correa-Metrio, A.Y., Ledru, M.-P., Mayle, F.E., Paduano, G., and Valencia, B.G., 2009. Millennial-scale ecological changes in tropical South America since the Last Glacial Maximum. In: Vimeux, F., Sylvestre, F. and Khodri M. (Eds.), *Past Climate Variability in South America and Surrounding Regions*. Springer, pp. 283-300.
- Urrego, D.H., Niccum, B.A., La Drew, C.F., Silman, M.R. and Bush, M.B., 2011. Fire and drought as drivers of early Holocene tree line changes in the Peruvian Andes. *Journal of Quaternary Science* 26, 28-36.
- Urrutia, R. and Vuille, M., 2009. Climate change projections for the tropical Andes using a regional climate model: temperature and precipitation simulations for the end of the 21st century. *Journal of Geophysical Research* 114. (Online) DOI: 10.1029/2008JD011021.

- Valencia, B.G., Urrego, D.H., Silman, M.R. and Bush, M.B., 2010. From ice age to modern: a record of landscape change in an Andean cloud forest. *Journal of Biogeography* 37, 1637-1647.
- Vandergoes, M.J., Newnham, R.M., Preusser, F., Hendy, C.H., Lowell, T.V., Fitzsimons, S.J., Hogg, A.G., Kasper, H.U. and Schluchter, C., 2005. Regional insolation forcing of late Quaternary climate change in the Southern Hemisphere. *Nature* 436, 242-245.
- van Hardenbroek, M., Heiri, O., Grey, J., Bodelier, P., Verbruggen, F. and Lotter, A., 2010. Fossil chironomid  $\delta^{13}\text{C}$  as a proxy for past methanogenic contribution to benthic food webs in lakes? *Journal of Paleolimnology* 43, 235-245.
- Velle, G., Brodersen, K.P., Birks, H.J.B. and Willassen, E., 2010. Midges as quantitative temperature indicator species: Lessons for palaeoecology. *The Holocene* 20, 989-1002.
- Vera, C., Higgins, W., Amador, J., Ambrizzi, T., Garreaud, R., Gochis, D., Gutzler, D., Lettenmaier, D., Marengo, J., Mechoso, C.R., Nogues-Paegle, J., Silva Dias, P.L. and Zhang, C., 2006. Toward a unified view of the American monsoon systems. *Journal of Climate* 19, 4977-5000.
- Verbruggen, F., Heiri, O., Reichert, G. J. and Lotter, A.F., 2010. Chironomid  $\delta^{18}\text{O}$  as a proxy for past lake water  $\delta^{18}\text{O}$ : a Lateglacial record from Rotsee (Switzerland). *Quaternary Science Reviews* 29, 2271-2279.
- Vergara, W., 2007. Economic impacts of rapid glacier retreat in the Andes. *EOS, Transactions, American Geophysical Union* 88, 261-268.
- Verissimo, A., Cochrane, M.A. and Souza, C., 2002. National forests in the Amazon. *Science* 297, 1478.
- Verschuren, D. and Eggermont, H., 2006. Quaternary paleoecology of aquatic Diptera in tropical and Southern Hemisphere regions, with special reference to the Chironomidae. *Quaternary Science Reviews* 25, 1926-1947.
- Verschuren, D., Tibby, J., Sabbe, K. and Roberts, N., 2000. Effects of depth, salinity, and substrate on the invertebrate community of a fluctuating tropical lake. *Ecology* 81, 164-182.
- Vidal, J., 2011. Bolivia enshrines natural world's rights with equal status for Mother Earth. In: *The Guardian* (newspaper), London, 11<sup>th</sup> April, 2011, pp. 15.

## References

- von Post, L., 1929. Die Zeichenschrift der Pollenstatistik. Geologiska Föreningens i Stockholm Förhandlingar 4, 543–565.
- von Post, L., 1946. The Prospect for pollen analysis in the study of the Earth's climatic history. *New Phytologist* 45, 193-193.
- Vuille, M. and Bradley, R.S., 2000. Mean annual temperature trends and their vertical structure in the tropical Andes. *Geophysical Research Letters* 27, 3885-3888.
- Vuille, M. and Werner, M., 2005. Stable isotopes in precipitation recording South American summer monsoon and ENSO variability: observations and model results. *Climate Dynamics* 25, 401-413.
- Wachtel, N., 1982. The Mitimaes of the Cochabamba Valley: the colonization policy of Huayna Capac. In: Collier, G. Rosaldo, R. and Wirth, J. (Eds.), *The Inca and Aztec States 1400-1800*. Academic, New York, pp. 199-235.
- Wagner, W.L., 2007. Revised classification of the Onagraceae. American Society of Plant Taxonomists, Ann Arbor, Michigan.
- Walker, I.R., 1987. Chironomidae (Diptera) in paleoecology. *Quaternary Science Reviews* 6, 29-40.
- Walker, I.R., 2001. Midges: Chironomids and related Diptera. In: Smol, J.P., Birks, H.J.H. and Last, W.M. (Eds.), *Tracking environmental change using lake sediments*. Kluwer Academic Publishers, London, pp. 43-66.
- Walker, I.R., Mott, R.J. and Smol, J.P., 1991. Allerød-Younger Dryas lake temperatures from midge fossils in Atlantic Canada. *Science* 253, 1010-1012.
- Walker, I.R., Wilson, S.E. and Smol, J.P. 1995. Chironomidae (Diptera): quantitative paleosalinity indicators for lakes of Western Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 52, 950–960.
- Walther, G.R., Beißner, S. and Burga, C.A., 2005. Trends in the upward shift of alpine plants. *Journal of Vegetation Science* 16, 541-548.
- Walsh, M.K., Whitlock, C. and Bartlein, P.J., 2008. A 14,300year long record of fire-vegetation-climate linkages at Battle Ground Lake, southwestern Washington. *Quaternary Research* 70, 251-264.
- Weckström, K., Weckström, J., Yliniemi, L.M. and Korhola, A., 2010. The ecology of *Pediastrum* (Chlorophyceae) in subarctic lakes and their potential as paleobioindicators. *Journal of Paleolimnology* 43, 61-73.

- Weng, C., Bush, M.B. and Chepstow-Lusty, A.J., 2004. Holocene changes of Andean alder (*Alnus acuminata*) in highland Ecuador and Peru. *Journal of Quaternary Science* 19, 685-691.
- Weng, C., Bush, M.B., Curtis, J.H., Kolata, A.L., Dillehay, T.D. and Binford, M.W., 2006. Deglaciation and Holocene climate change in the western Peruvian Andes. *Quaternary Research* 66, 87-96.
- Whitlock, C. and Larsen, C. 2001. Charcoal as fire proxy. In: Smol, J.P, Birks, H.J.B. and Last, W.M. (Eds.), *Tracking environmental change using lake sediments: Volume 3: terrestrial, algal, and siliceous indicators*. Kluwer Academic Publishers, Dordrecht, pp. 75-97.
- Whitlock, C. and Millspaugh, S.H., 1996. Testing the assumptions of fire-history studies: an examination of modern charcoal accumulation in Yellowstone National Park, USA. *The Holocene* 6, 7-15.
- Wick, L., Lemcke, G. and Sturm, M., 2003. Evidence of Lateglacial and Holocene climatic change and human impact in eastern Anatolia: high-resolution pollen, charcoal, isotopic and geochemical records from the laminated sediments of Lake Van, Turkey. *The Holocene* 13, 665-675.
- Wiederholm, T., 1983. Chironomidae of the Holarctic region. Keys and diagnoses. Part 1. Larvae. *Entomologica Scandinavica. Supplement* 19, 1–457.
- Wille, M., Hooghiemstra, H., Hofstede, R., Fehse, J. and Jan, S., 2002. Upper forest line reconstruction in a deforested area in northern Ecuador based on pollen and vegetation analysis. *Journal of Tropical Ecology* 18, 409-440.
- Williams, J.J., 2011 Human and climate impacts on Tropical Andean ecosystems. Unpublished PhD thesis. The Open University, Milton Keynes.
- Williams, J.J., Gosling, W.D., Coe, A.L., Brooks, S.J. and Gulliver, P., 2011. Four thousand years of environmental change and human activity in the Cochabamba Basin, Bolivia. *Quaternary Research (Online)*. DOI: 10.1016/j.yqres.2011.03.004.
- Willis, K.J., Bailey, R.M., Bhagwat, S.A. and Birks, H.J.B., 2010. Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data. *Trends in Ecology & Evolution* 25, 583-591.
- Willis, K.J. and Birks, H.J.B., 2006. What Is Natural? The need for a long-term perspective in biodiversity conservation. *Science* 314, 1261 -1265.

## References

- Winterhalder, B., Larsen, R. and Thomas, R., 1974. Dung as an essential resource in a highland Peruvian community. *Human Ecology* 2, 89-104.
- Woodward, C.A. and Shulmeister, J., 2005. A Holocene record of human induced and natural environmental change from Lake Forsyth (Te Wairewa), New Zealand. *Journal of Paleolimnology* 34, 481-501.
- World Bank, 1994. Bolivia: household rural energy strategy, 62/94, Washington D.C.
- Wright, H.E., Mann, D.H. and Glaser, P.H., 1984. Piston corers for peat and lake sediments. *Ecology* 65, 657-659.
- Ybert, J.P., 1992. Ancient lake environments as deduced from pollen analysis. In: Dejoux, C. and Iltis, A. (Eds.), *Lake Titicaca. a synthesis of limnological knowledge*. Kluwer Academic Publishing, Dordrecht, pp. 49-60.
- Yevich, R. and Logan, J.A., 2003. An assessment of biofuel use and burning of agricultural waste in the developing world. *Global Biogeochem Cycles* 17, 1095-1135.
- Young, B.E., 2007. Endemic species distributions on the east slope of the Andes in Peru and Bolivia. NatureServe, Arlington, Virginia.
- Young, K.R., Leon, B., Cano, A. and Herrera-MacBryde, O., 1997. Peruvian Puna Peru. In: Davis, S.D., Heywood, V.H., Herrera-MacBryde, O., Villa-Lobos, J. and Hamilton, A.C. (Eds.), *Centres of plant diversity: a guide and strategy for their conservation*, Volume 3: The Americas. IUCN, WWF, Oxford.
- Young, K., Ulloa, C., Luteyn, J. and Knapp, S., 2002. Plant evolution and endemism in Andean South America: an introduction. *The Botanical Review* 68, 4-21.
- Young-Sanchez, M., 2004. *Tiwanaku: Ancestors of the Inca*. Denver Art Museum and University of Nebraska Press, Lincoln.
- Zech, J., Zech, R., May, J.H., Kubik, P.W. and Veit, H., 2010. Lateglacial and early Holocene glaciation in the Tropical Andes caused by La Niña-like conditions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 293, 248-254.
- Zech, R., Kull, C., Kubik, P.W., and Veit, H., 2007. LGM and Late Glacial glacier advances in the Cordillera Real and Cochabamba (Bolivia) deduced from <sup>10</sup>Be surface exposure dating. *Climate of the Past* 3, 623-635.

- Zech, R., Smith, J., and Kaplan, M.R., 2009. Chronologies of the Last Glacial Maximum and its termination in the Andes (~10–55°S) based on surface exposure dating. In: Vimeux, F., Sylvestre, F. and Khodri M. (Eds.), Past Climate Variability in South America and Surrounding Regions. Springer, pp. 61-87.
- Zhou, J. and Lau, K. M., 1998. Does a monsoon climate exist over South America? Journal of Climate 11, 1020-1040.
- Zimmerer, K.S., 1993. Soil erosion and labour shortages in the Andes with special reference to Bolivia, 1953-1991: Implications for "conservation-with-development". World Development 21, 1659-1675.
- Zimmerer, K.S., 2000. Rescaling irrigation in Latin America: the cultural images and political ecology of water resources. Cultural Geographies 7, 150-175.
- Zimmermann, H., Renison, D., Leyer, I., and Hensen, I., 2009. Do we need livestock grazing to promote *Polylepis australis* tree recruitment in the Central Argentinean Mountains? Ecological Research 24, 1075-1081.

## Appendix A1) Initial core description

This appendix presents the detailed core description for all sediments analysed for this thesis. The methods of description are discussed, followed by images of all core drives extracted.

---

### A1.1) Description methodology and key

In the following initial core descriptions (Plates A1.1 and A1.2), depths are displayed in reference to the individual drive lengths and also to the relative depth below the lake floor (blf). All depths are presented as centimetres and sections of fine banding are expanded for easier viewing. Radiometric dates obtained from cores are marked. Detailed information for each radiometric date is provided in Appendix A3.

Initial core description was completed with reference to the Troels-Smith sediment description system (Birks and Birks, 1980), and the Munsell Soil Colour Charts (Munsell Soil Color Charts, 2000). An explanation of the codes utilised in this thesis is provided in Tables A1.1 and A1.2

Sediment composition	
<b>As</b>	Argilla steatodes - clay Particles < 0.002 mm
<b>Dh</b>	Detritus herbosus - plant material Fragments > 2 mm
<b>Ga</b>	Grana arenosa - fine sand Particles 0.06 – 0.002 mm
<b>Ld</b>	Limus detrituosus - lake mud, elastic, non-sticky Fragments < 0.1 mm

**Table A1.1** Key to sediment compositions codes used in core profile logs. Following the Troels-Smith sediment description system (Birks and Birks, 1980).



Sediment colour			
<b>10YR: 2/1</b>	black	<b>Gley 1: 2.5/N</b>	black
<b>10YR: 2/2</b>	very dark brown	<b>Gley 1: 3/10Y</b>	very dark greenish grey
<b>10YR: 3/1</b>	very dark grey	<b>Gley 1: 3/N</b>	very dark grey
<b>10YR: 3/2</b>	very dark greyish brown	<b>Gley 1: 4/10Y</b>	dark greenish grey
<b>10YR: 4/1</b>	dark grey	<b>Gley 1: 4/N</b>	dark grey
<b>10YR: 4/2</b>	dark greenish brown	<b>Gley 1: 5/10Y</b>	greenish grey
<b>10YR: 5/1</b>	grey	<b>Gley 1: 5/N</b>	grey
<b>10YR: 5/2</b>	greyish brown	<b>Gley 1: 6/10GY</b>	greenish grey
<b>10YR: 6/1</b>	grey	<b>Gley 1: 6/N</b>	grey
<b>10YR: 6/2</b>	light brownish grey	<b>Gley 1: 7/10Y</b>	light greenish grey
<b>10YR: 7/1</b>	light grey	<b>Gley 1: 7/N</b>	light grey
<b>10YR: 8/1</b>	white		

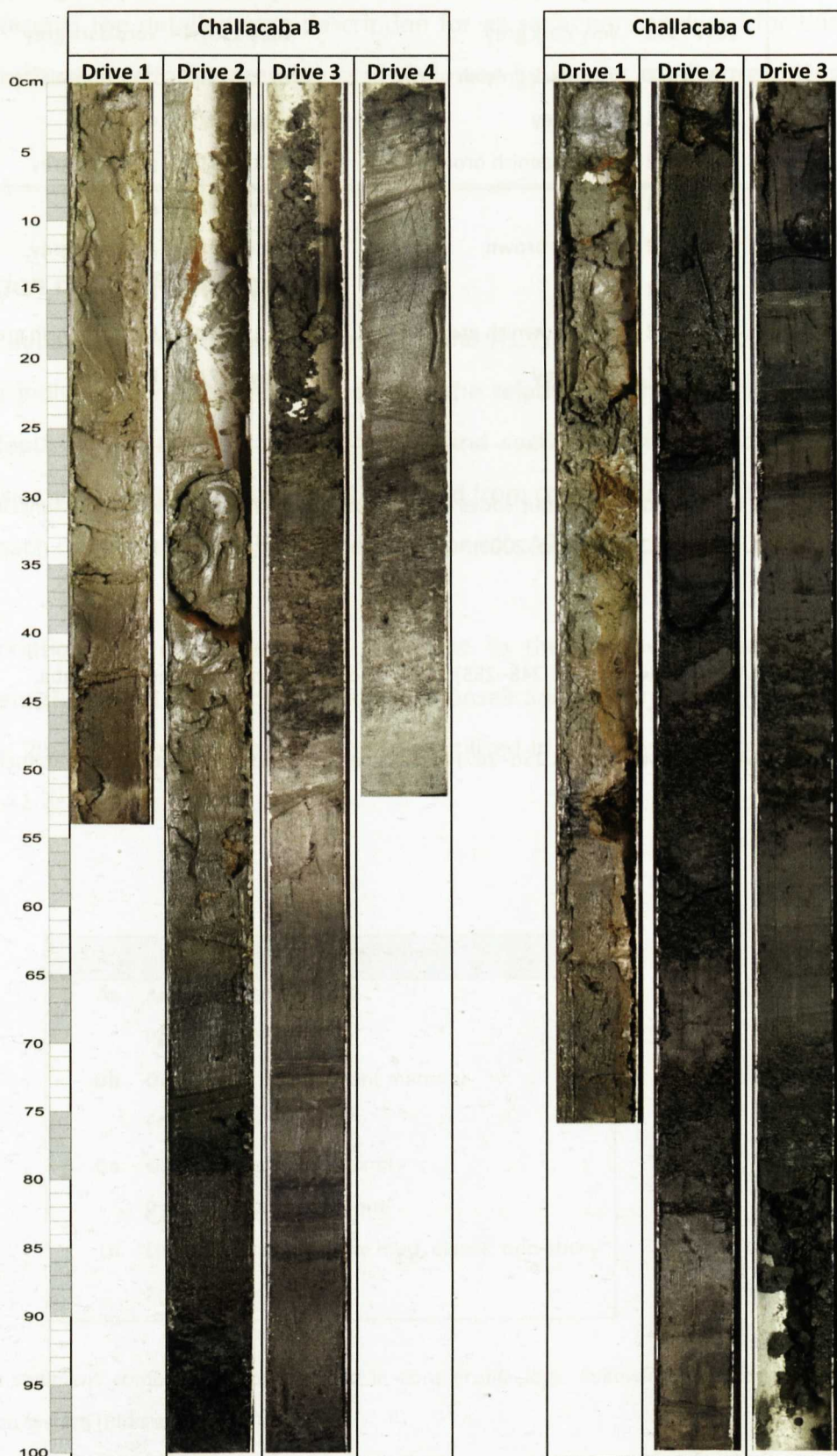
**Table A1.2** Key to sediment colour codes used in core profile logs. Following the Munsell Soil Colour Chart system (Munsell Soil Color Charts, 2000).

**Plate A1.1 A–H** (following pages 248–255) Initial core descriptions for Lake Challacaba.

**Plate A1.2 A–K** (following pages 256–267) Initial core descriptions for Laguna Khomer Kocha Upper.

## A1.2) Lake Challacaba

Vacas Lake District. 17° 33.257 S, 65° 34.024 W; 3419 m asl.



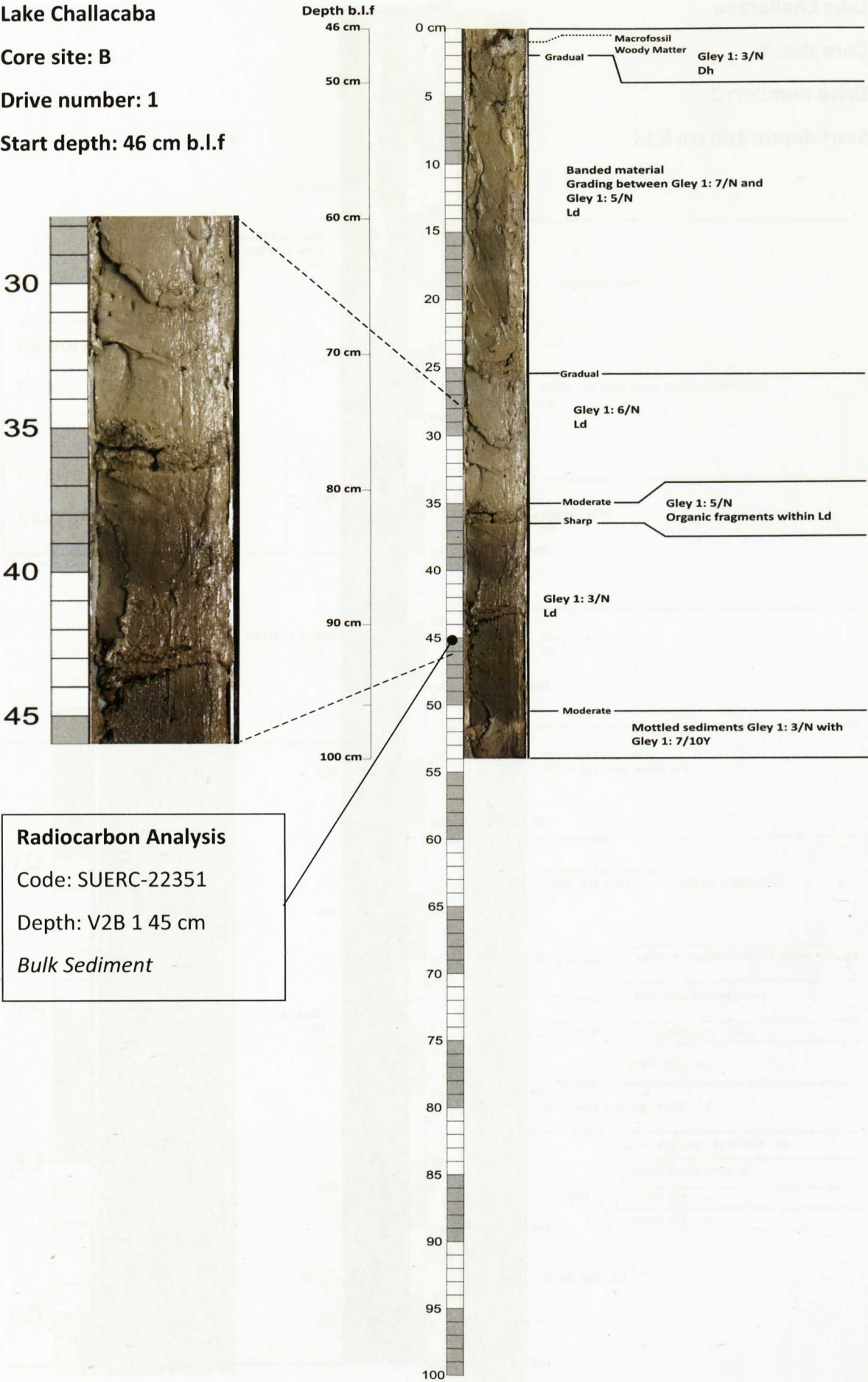


Lake Challacaba

Core site: B

Drive number: 1

Start depth: 46 cm b.l.f

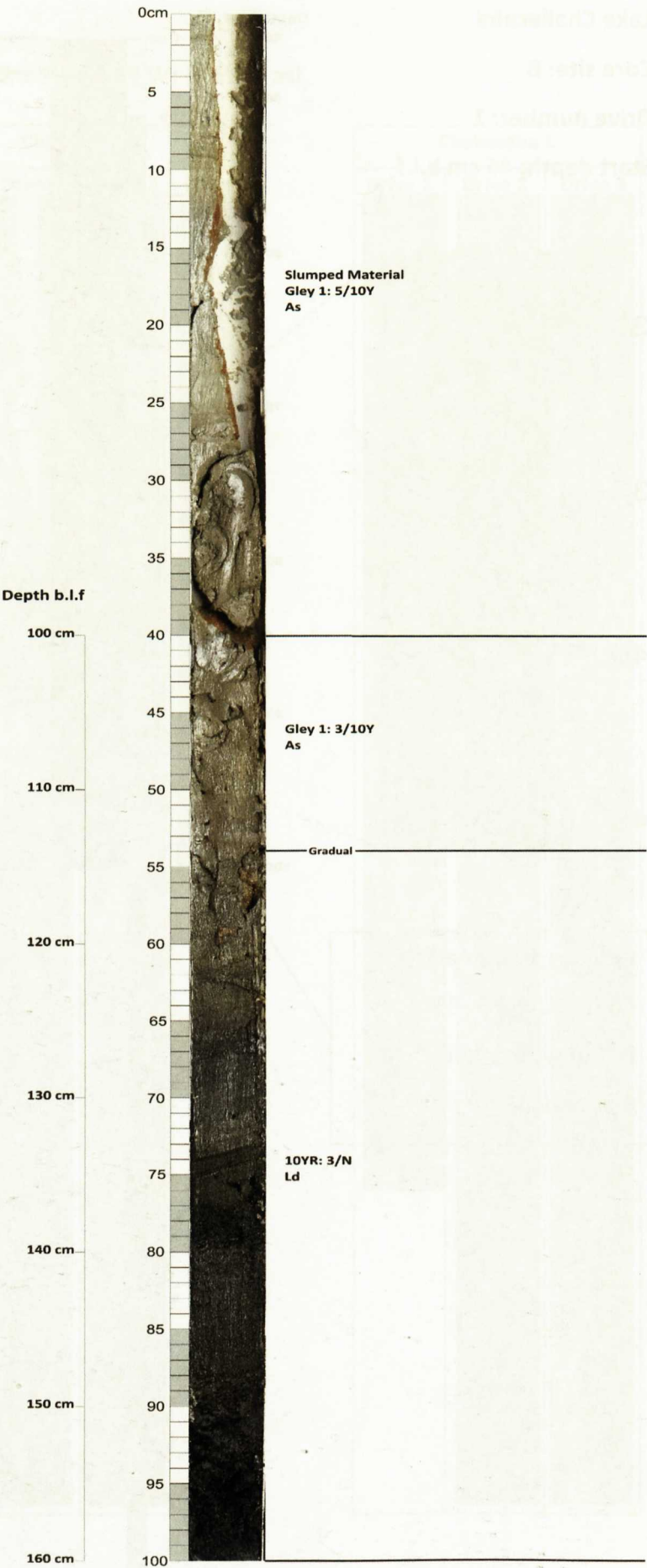


Lake Challacaba

Core site: B

Drive number: 2

Start depth: 100 cm b.l.f

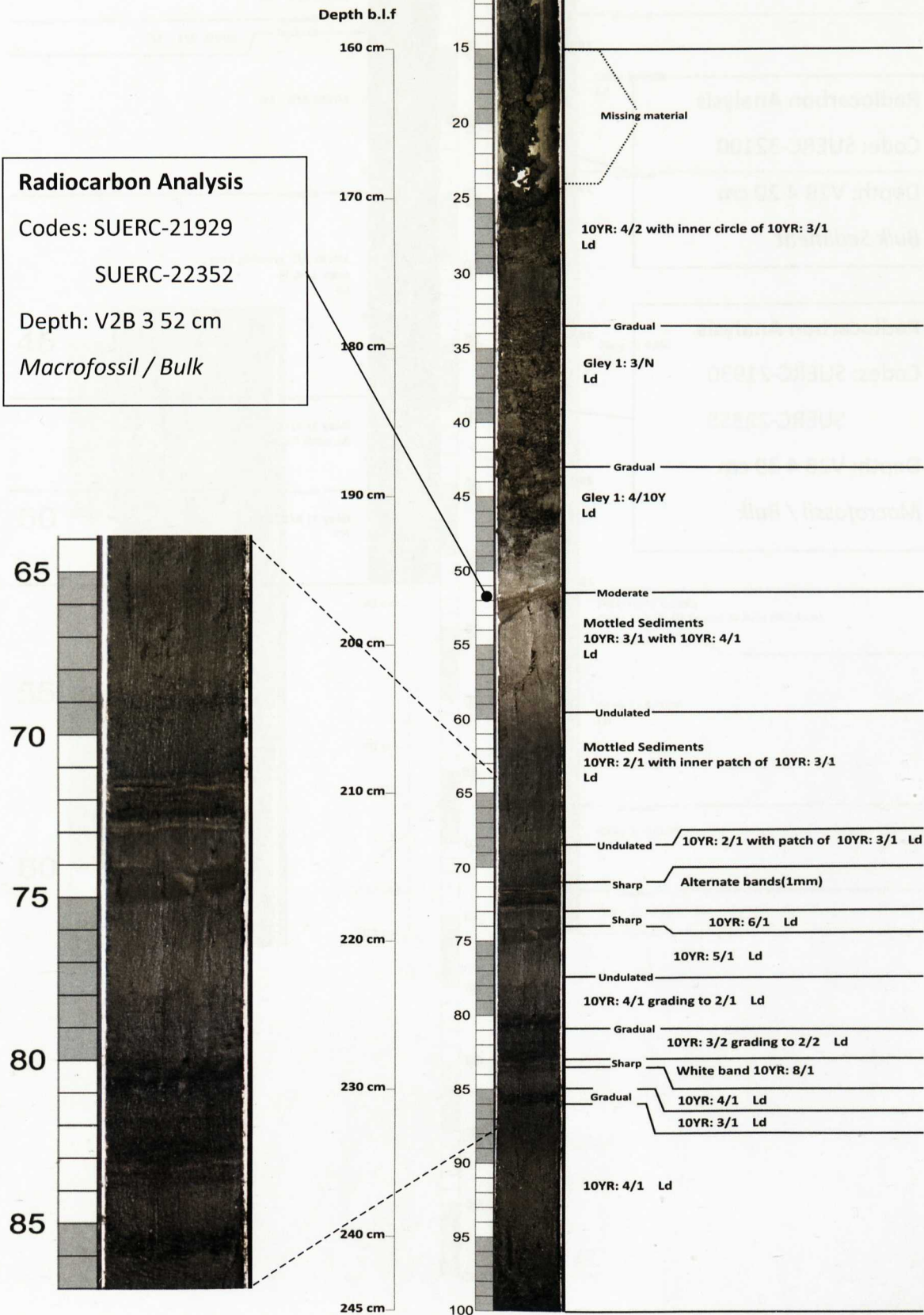


Lake Challacaba

Core site: B

Drive number: 3

Start depth: 160 cm b.l.f





Lake Challacaba

Core site: B

Drive number: 4

Start depth: 245 cm b.l.f

**Radiocarbon Analysis**

Code: SUERC-32100

Depth: V2B 4 20 cm

*Bulk Sediment*

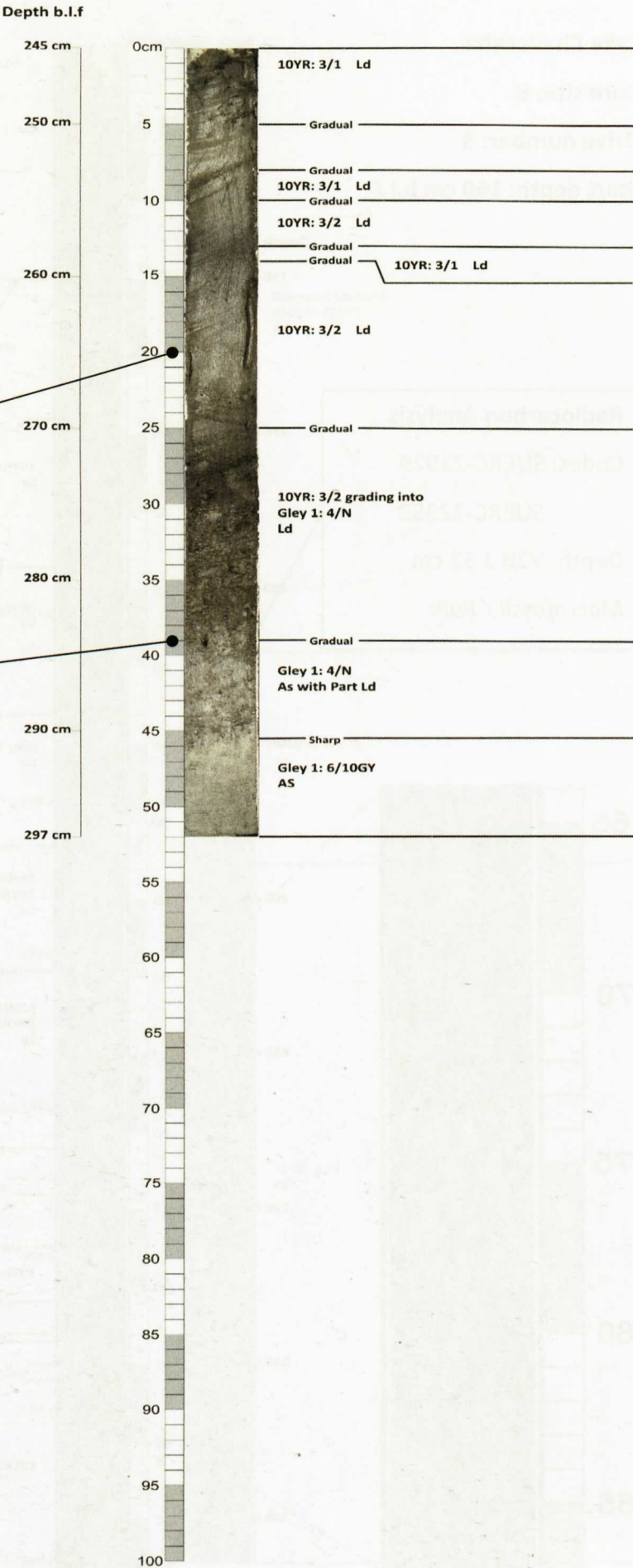
**Radiocarbon Analysis**

Codes: SUERC-21930

SUERC-22355

Depth: V2B 4 39 cm

*Macrofossil / Bulk*

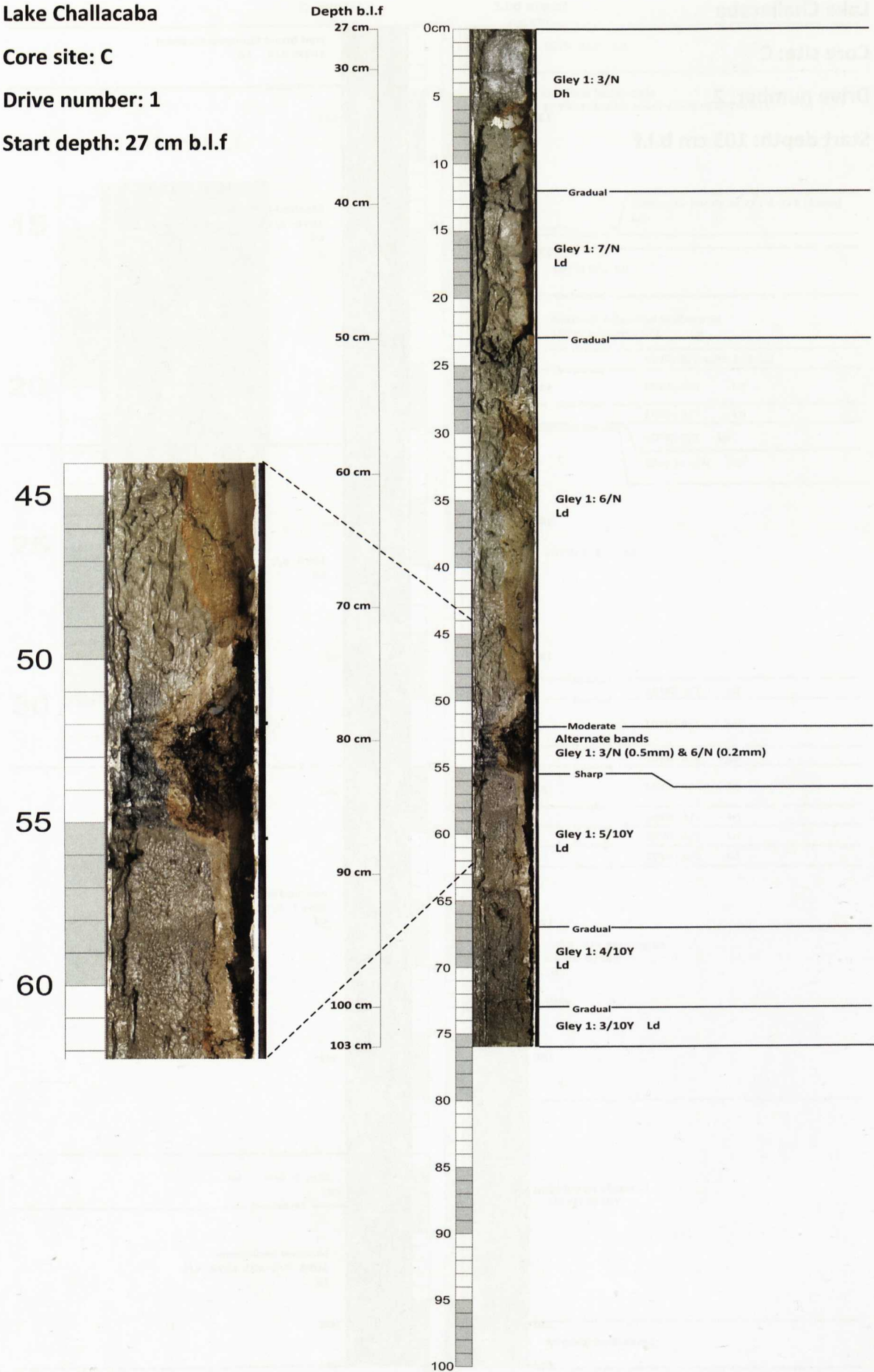


Lake Challacaba

Core site: C

Drive number: 1

Start depth: 27 cm b.l.f

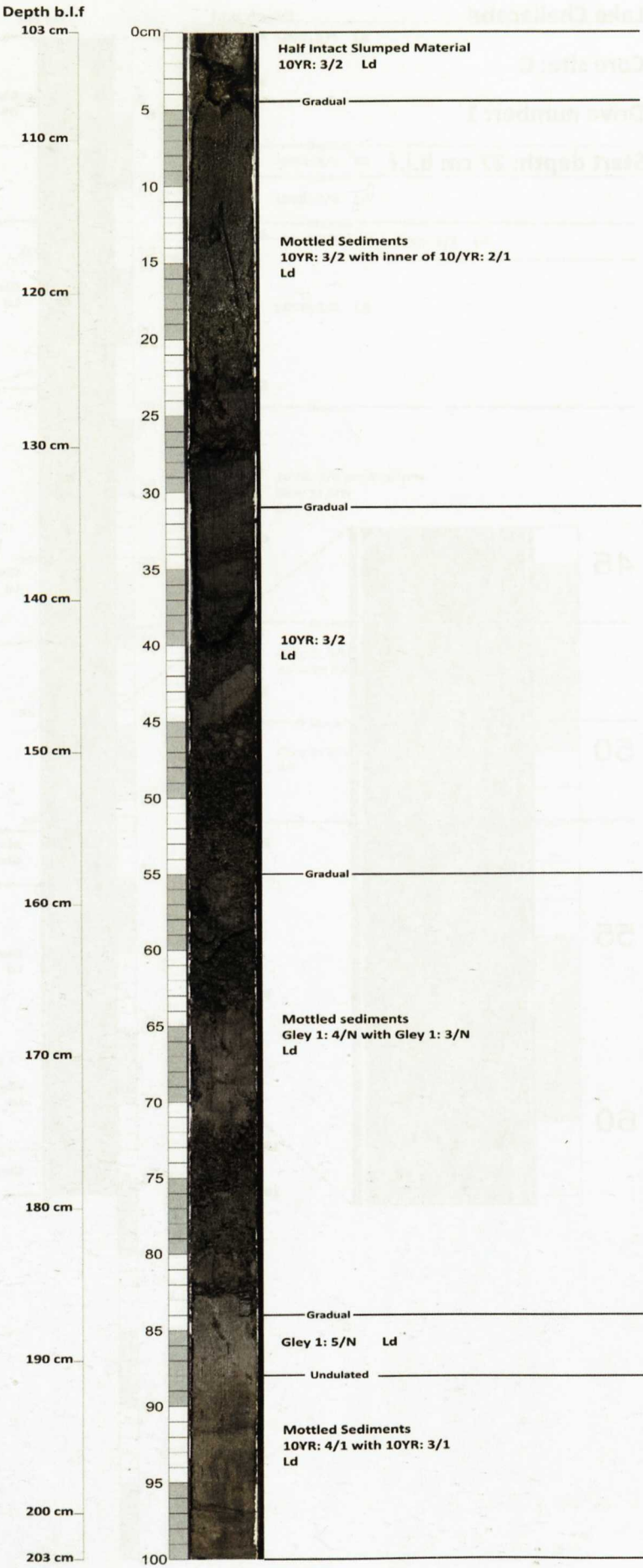


Lake Challacaba

Core site: C

Drive number: 2

Start depth: 103 cm b.l.f



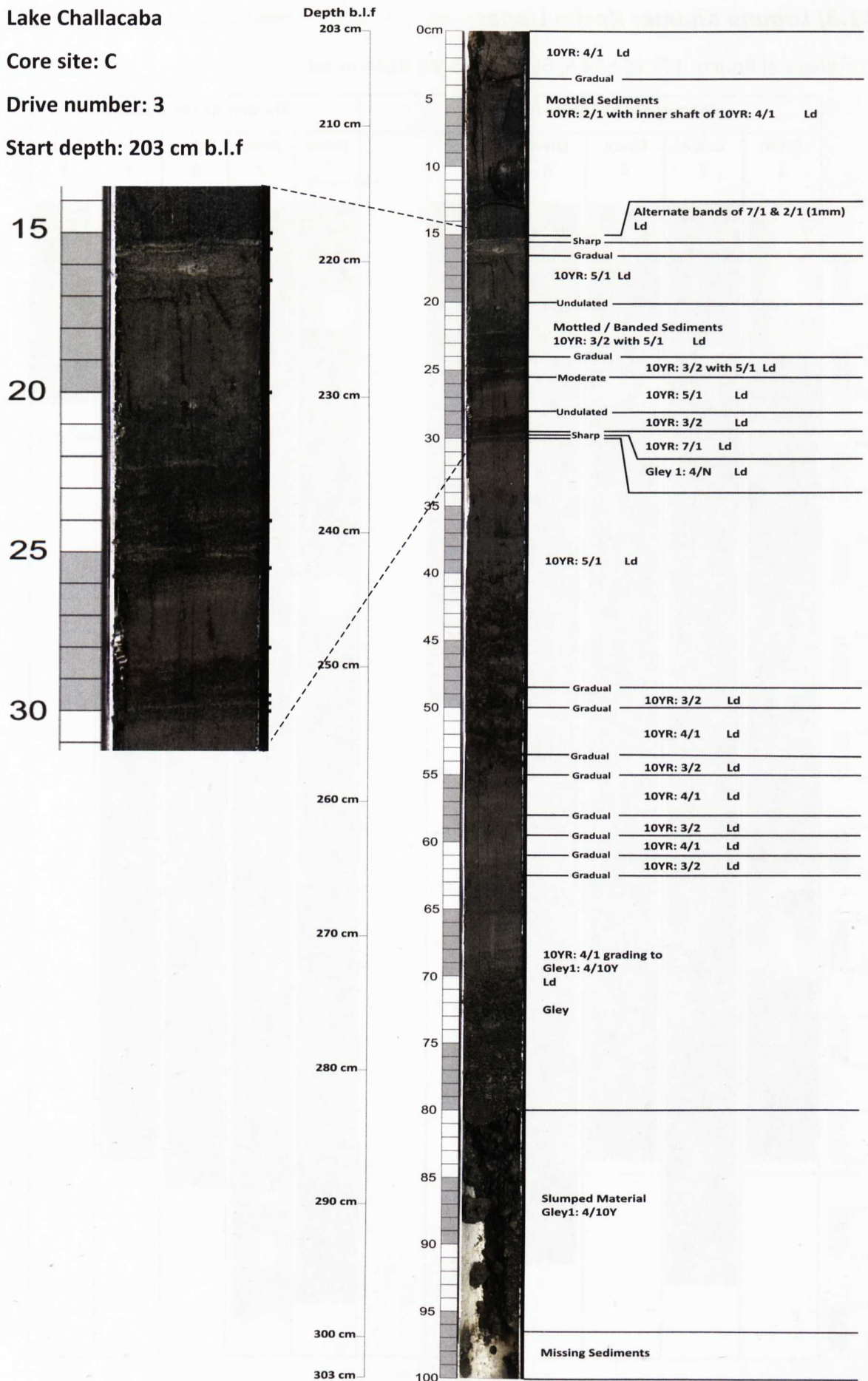


## Lake Challacaba

Core site: C

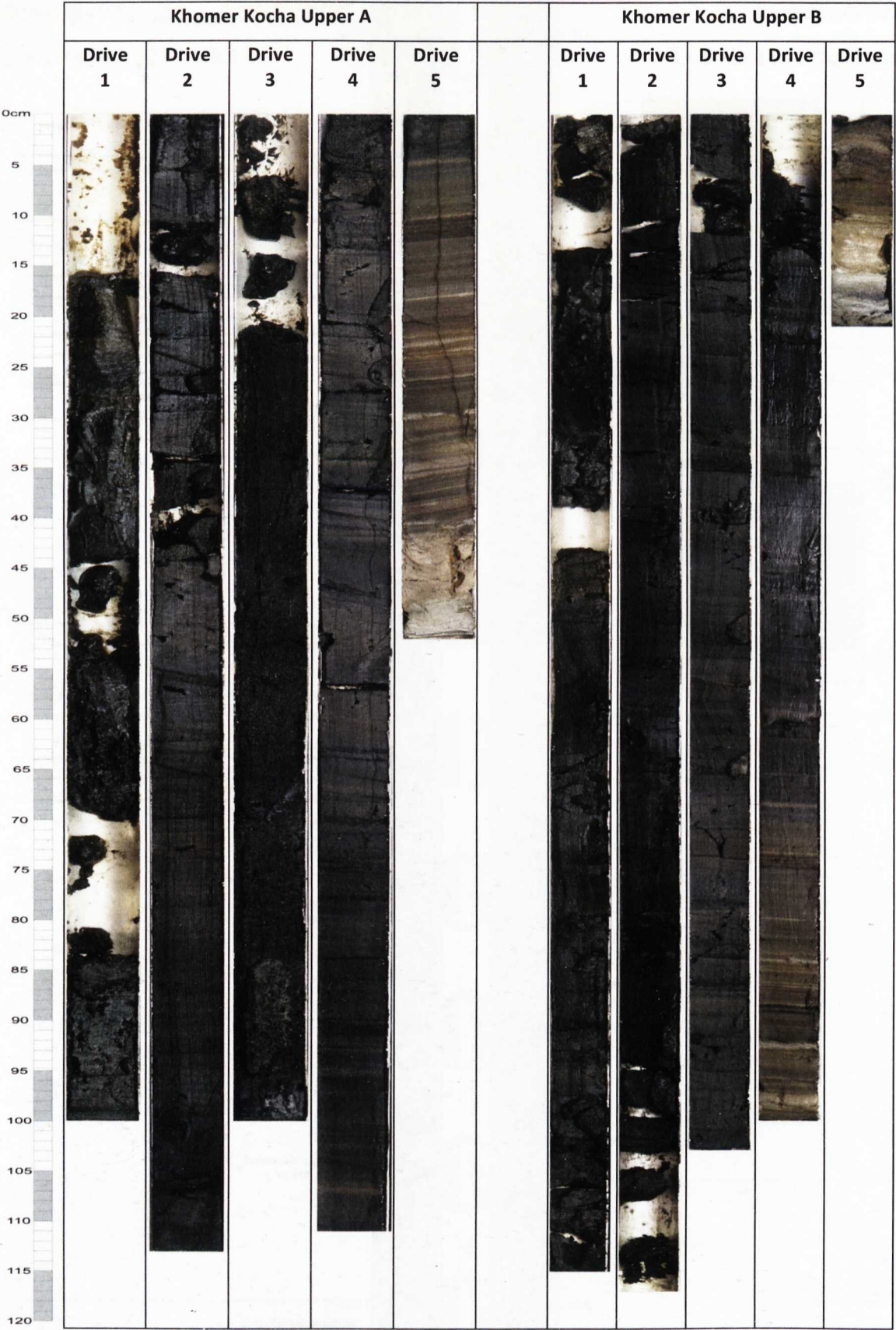
Drive number: 3

Start depth: 203 cm b.l.f



A1.3) Laguna Khomer Kocha Upper

Cordillera el Ronco. 17° 16.514 S, 65° 43.945 W; 4144 m asl



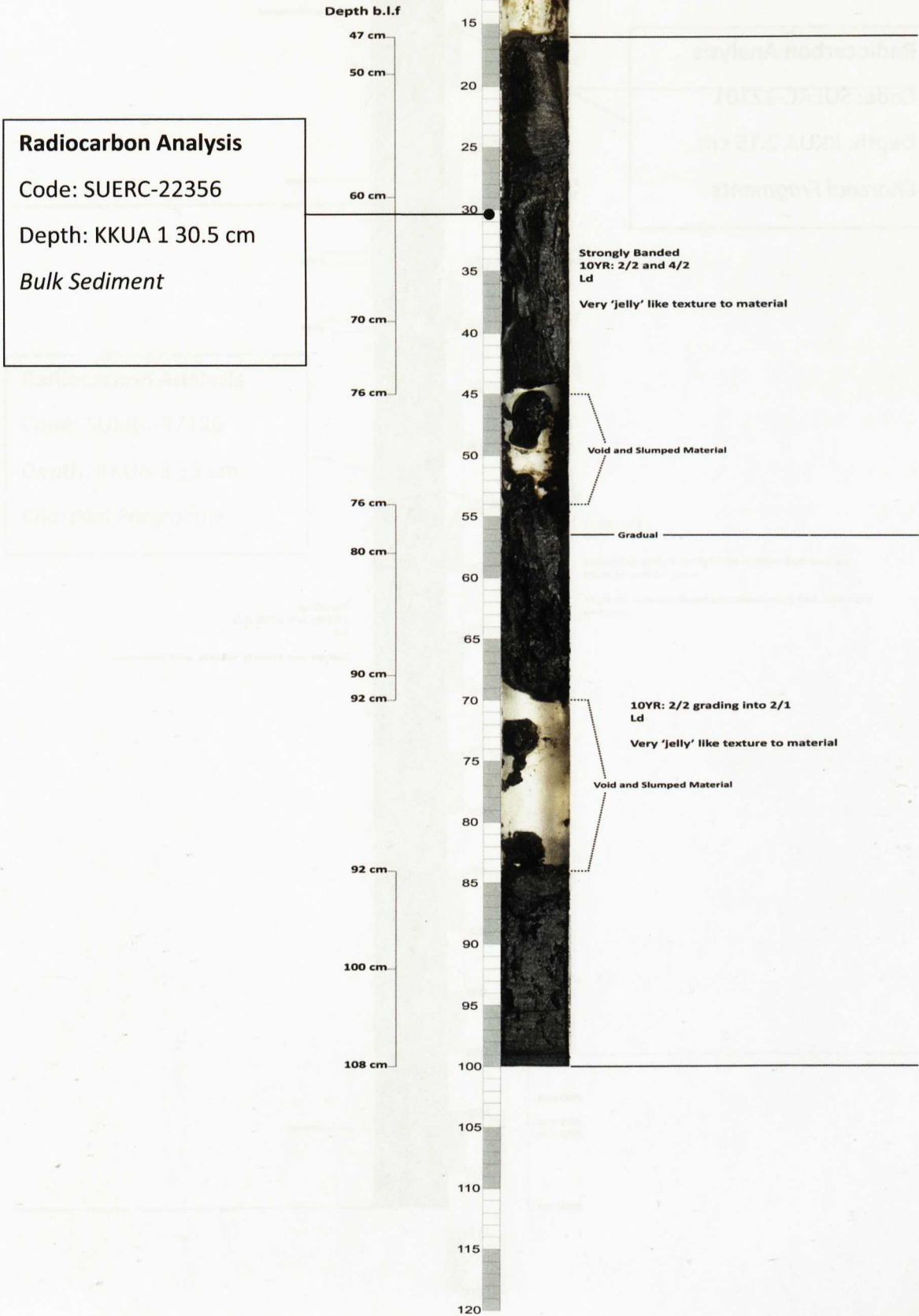


Laguna Khomer Kocha Upper

Core site: A

Drive number: 1

Start depth: 47 cm b.l.f



Laguna Khomer Kocha Upper

Core site: A

Drive number: 2

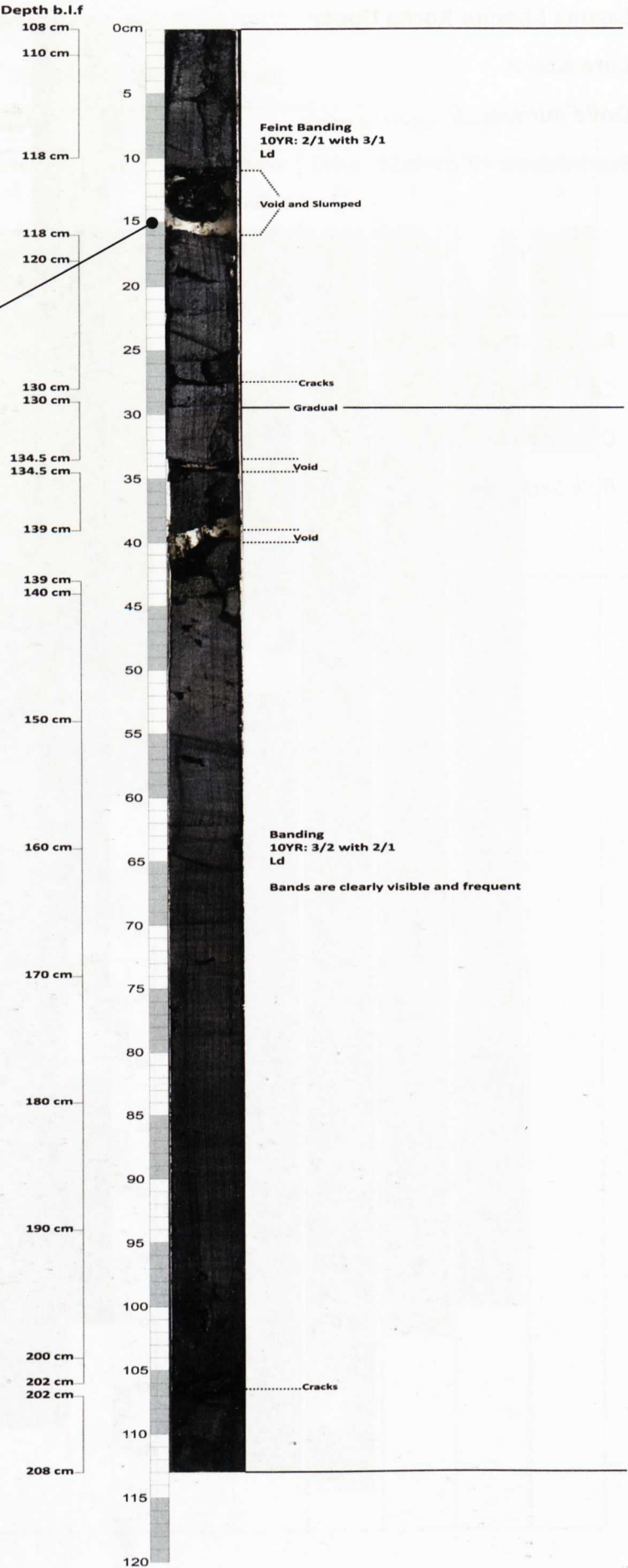
Start depth: 108 cm b.l.f

**Radiocarbon Analysis**

Code: SUERC-32101

Depth: KKUA 2 15 cm

*Charcoal Fragments*

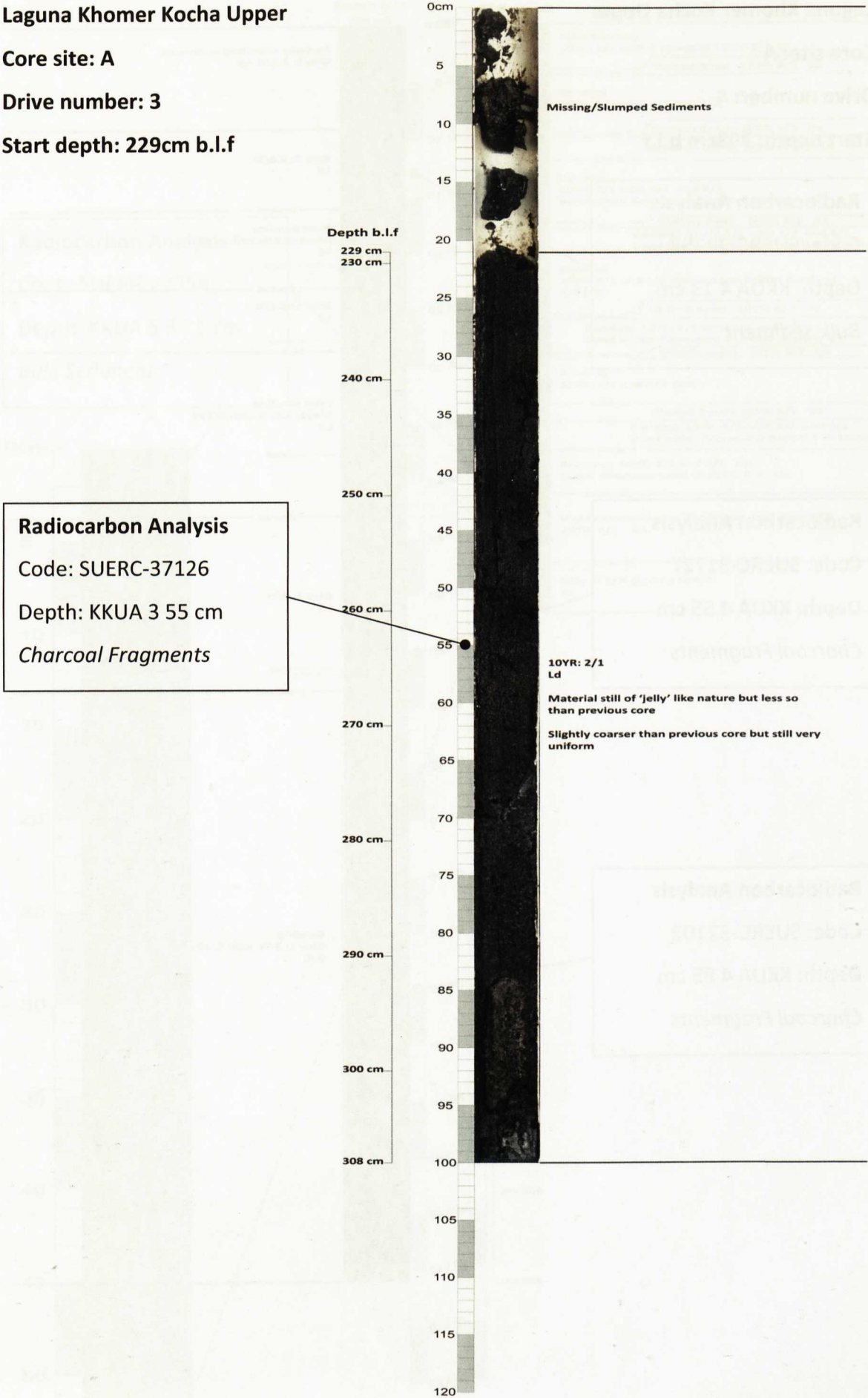


Laguna Khomer Kocha Upper

Core site: A

Drive number: 3

Start depth: 229cm b.l.f





Laguna Khomer Kocha Upper

Core site: A

Drive number: 4

Start depth: 308cm b.l.f

**Radiocarbon Analysis**

Code: SUERC-22357

Depth: KKUA 4 13 cm

*Bulk Sediment*

**Radiocarbon Analysis**

Code: SUERC-31727

Depth: KKUA 4 55 cm

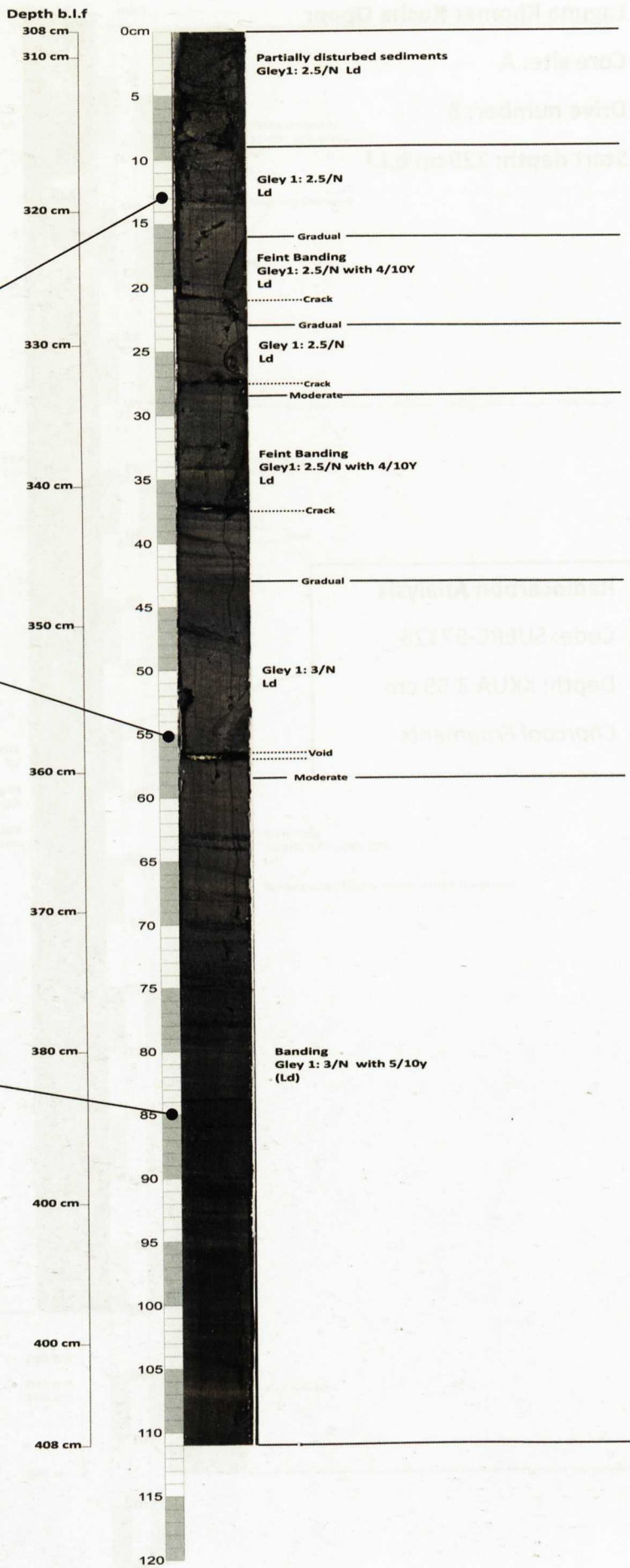
*Charcoal Fragments*

**Radiocarbon Analysis**

Code: SUERC-32102

Depth: KKUA 4 85 cm

*Charcoal Fragments*



Laguna Khomer Kocha Upper

Core site: A

Drive number: 5

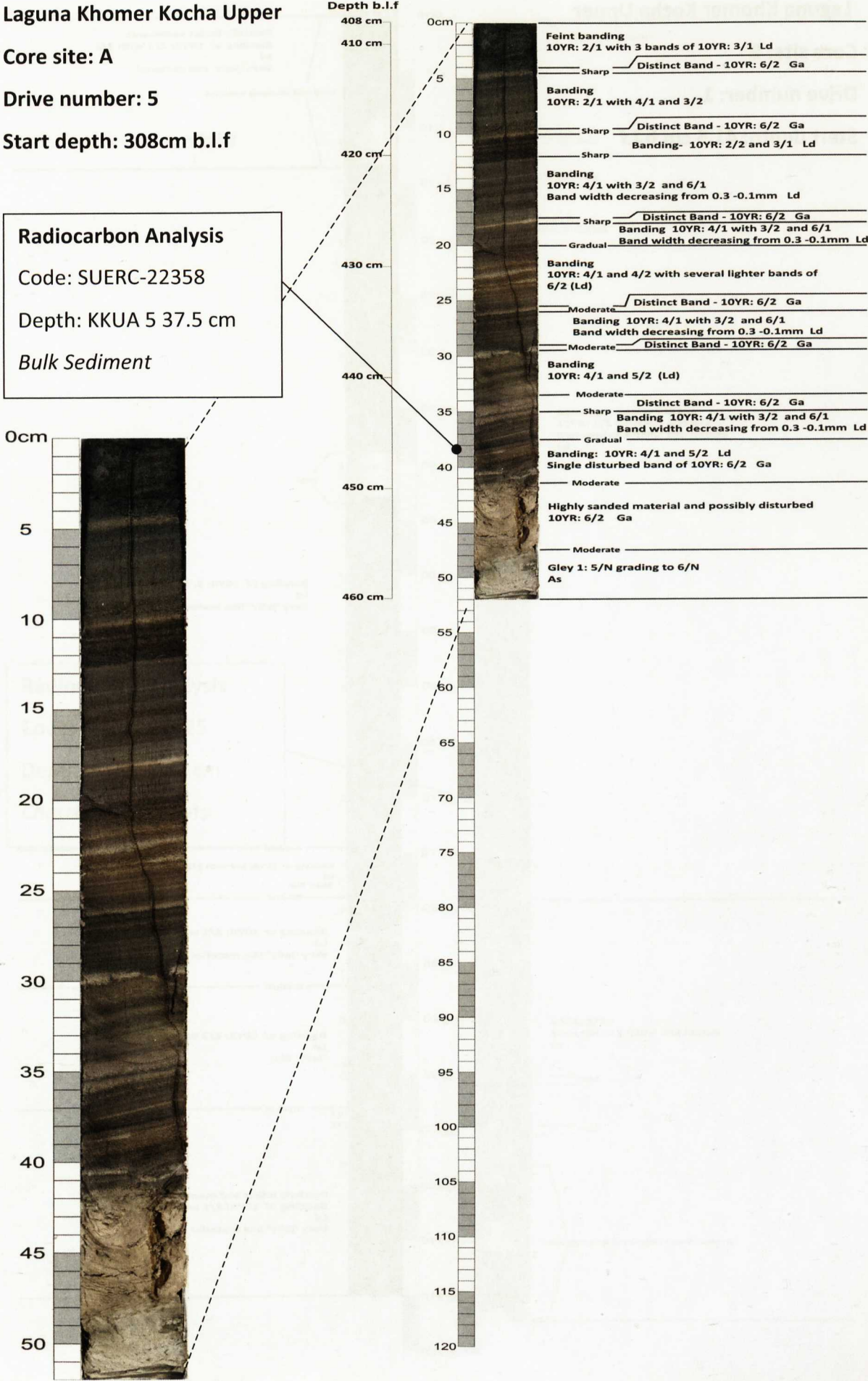
Start depth: 308cm b.l.f

**Radiocarbon Analysis**

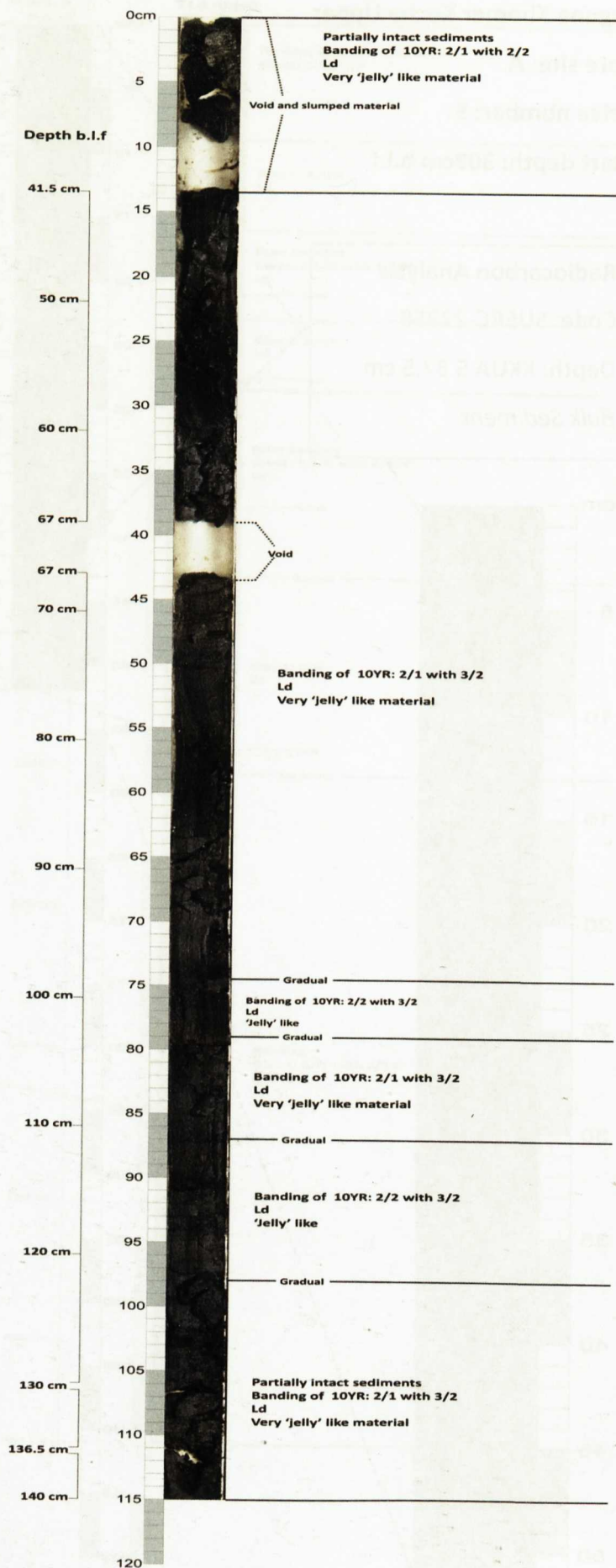
Code: SUERC-22358

Depth: KKUA 5 37.5 cm

*Bulk Sediment*





**Laguna Khomer Kocha Upper****Core site: B****Drive number: 1****Start depth: 41.5 cm b.l.f**



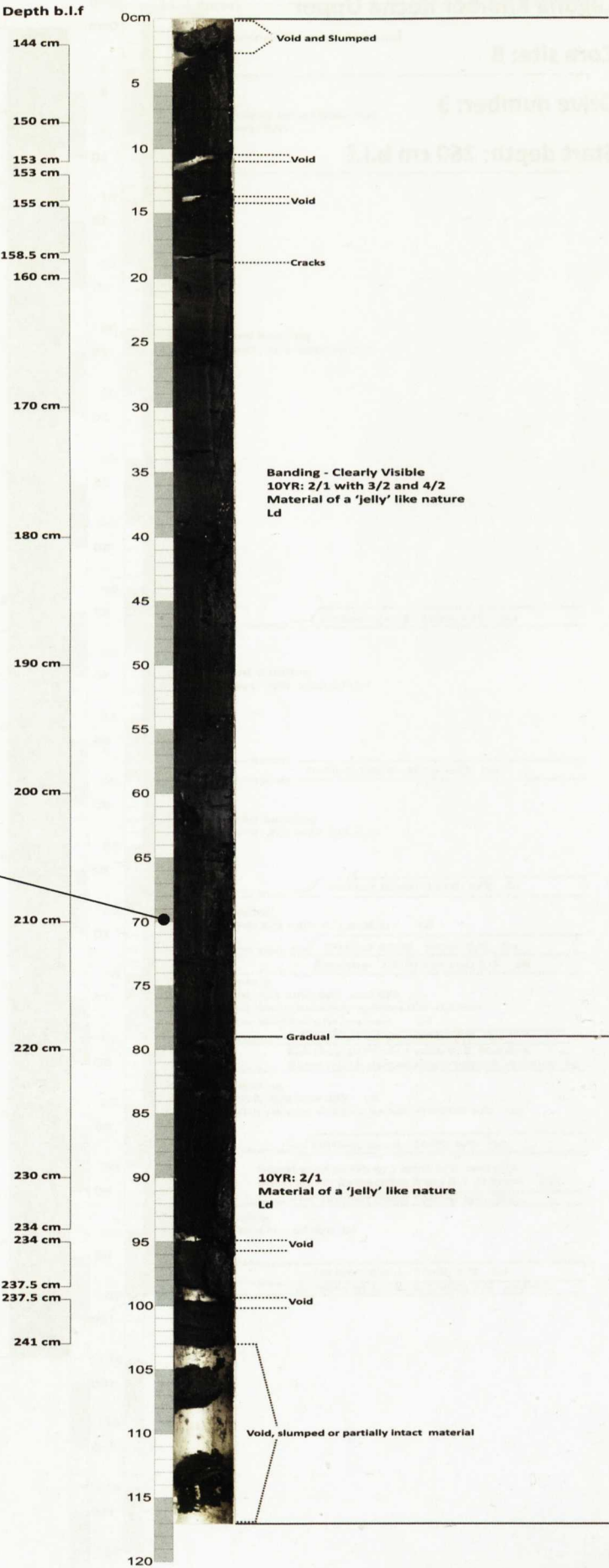
Laguna Khomer Kocha Upper

Core site: B

Drive number: 2

Start depth: 144 cm b.l.f

**Radiocarbon Analysis**  
Code: SUERC-31725  
Depth: KKUB 2 70 cm  
*Charcoal Fragments*

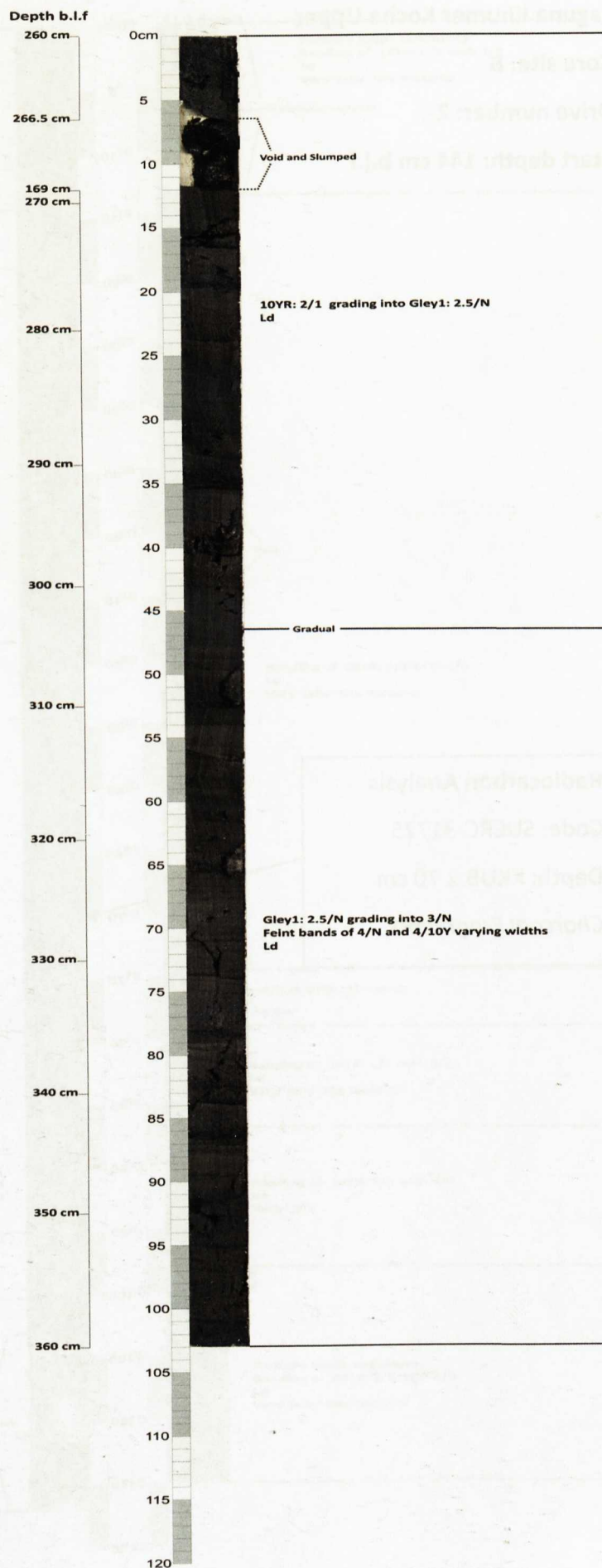


**Laguna Khomer Kocha Upper**

**Core site: B**

**Drive number: 3**

**Start depth: 260 cm b.l.f**

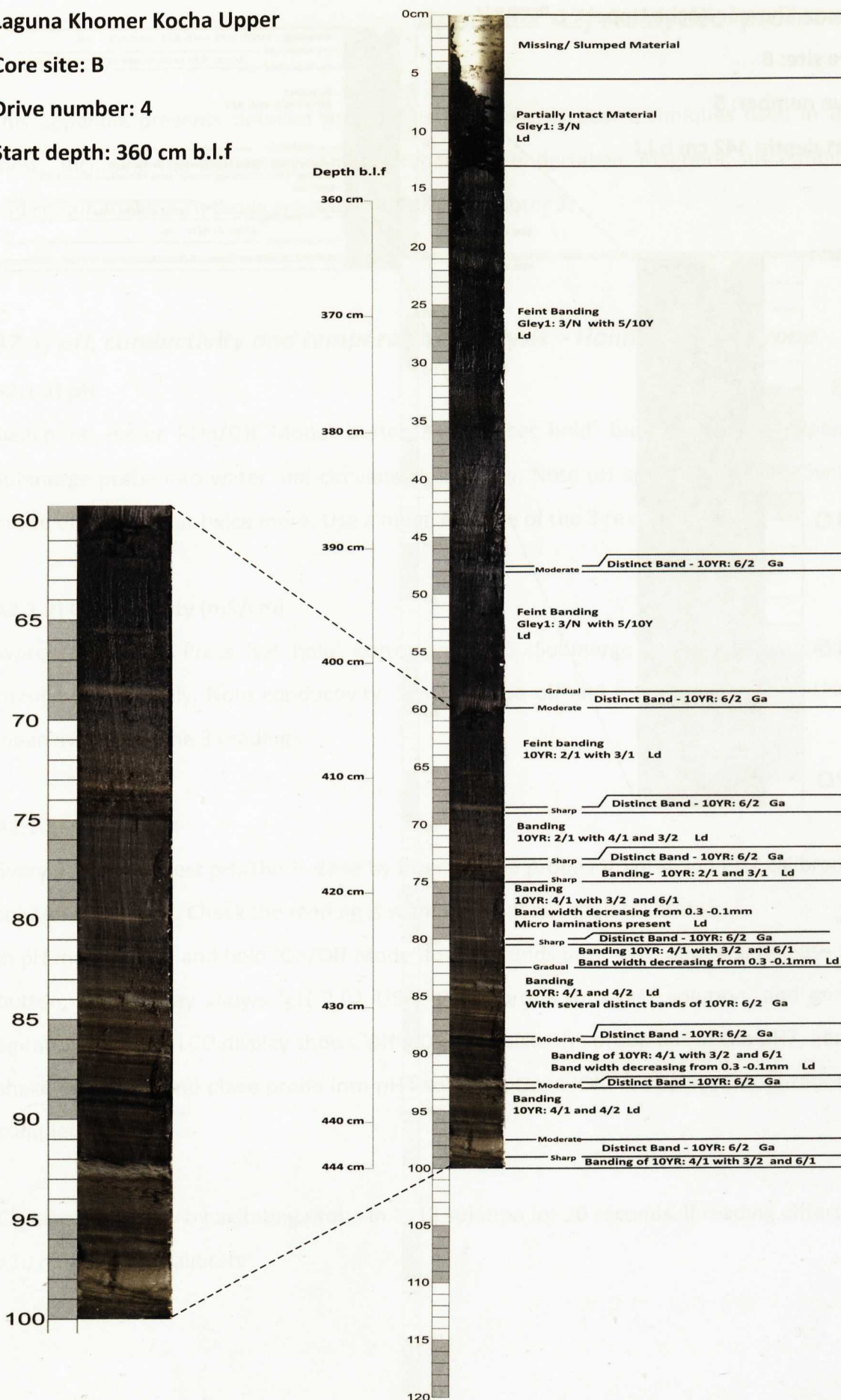


### Laguna Khomer Kocha Upper

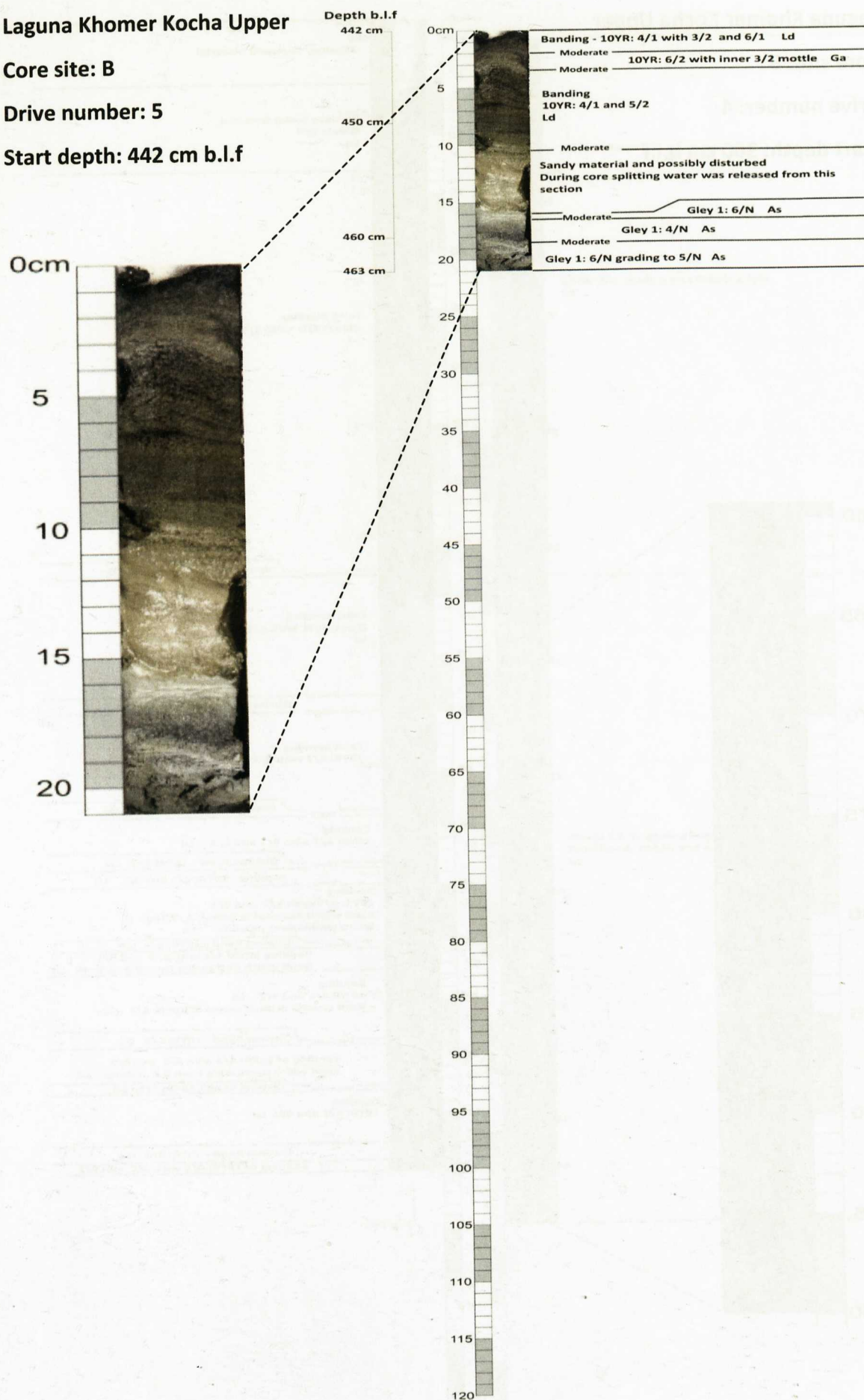
**Core site: B**

**Drive number: 4**

**Start depth: 360 cm b.l.f**





**Laguna Khomer Kocha Upper****Core site: B****Drive number: 5****Start depth: 442 cm b.l.f**

## **Appendix A2) Analytical protocols**

This appendix presents detailed procedures for the analytical techniques used in this thesis, including the laboratory sample preparation undertaken. Magnetic susceptibility and colour analysis methods are provided fully in Chapter 3.

---

### **A2.1) pH, conductivity and temperature analysis – Hanna 991300 Probe**

#### **A2.1.1) pH**

Switch on meter ('On/Off Mode' button). Press 'set hold' button until pH appears. Submerge probe into water and circulate thoroughly. Note pH and temperature. Switch probe off and repeat twice more. Use a mean average of the 3 readings.

#### **A2.1.2) Conductivity (mS/cm)**

Switch on meter. Press 'set hold' button until mS. Submerge probe into water and circulate thoroughly. Note conductivity. Switch probe off and repeat twice more. Use a mean average of the 3 readings.

#### **A2.1.3) Calibration**

Every 2 to 4 days test pH. This is done by inserting the probe into pH4 and pH7 calibration solutions provided. Check the reading is within  $\pm 0.1$ . If not then calibrate:

In pH mode, press and hold 'On/Off Mode' for 3 seconds until 'CAL' appears. Release the button, LCD display shows 'pH 7.01 USE'. Place probe into pH7 solution, and gently agitate. When the LCD display shows 'pH 4.01 USE', take the probe out of the pH7, gently shake any drops and place probe into pH4 solution. Once 'OK' is displayed, calibration is complete.

Check conductivity by agitating probe in 1413 solution for 20 seconds. If reading differs by  $>10$  mS/cm then calibrate:

In mS mode, press and hold 'On/Of Mode' button for 3 seconds, until 'CAL' appears. Release the button, LCD display shows 'mS 1413 USE'. Place probe into 1413 solution. Once 'OK' is displayed, calibration is complete.

This protocol was adapted from one provided by S.J.Brooks.

## **A2.2) Core tube splitting**

### **A2.2.1) Set up**

Ensure that work surface and plastic bed to hold tube are secure and clean. Secure and check that the titanium bit is correctly fitted to the router. Set router speed to "1" and ensure router slides freely along the plastic bed in both directions (lubricate if necessary). Attach vacuum cleaner to router ensuring hose of cleaner does not impede the movement of router along plastic bed. Place the core tube in to the plastic tube bed securing both ends firmly with the inserts appropriate for the core tube diameter.

### **A2.2.2) Cutting**

Set height limiter on router against the highest point on the core tube wall ensuring that the depth adjuster is extended to its maximum position. Lubricate router bit and lower plastic guard into place. With the vacuum cleaner on, start the router and depress the blade until you reach the limit set. Starting from one end, push the router slowly and smoothly along the length of the core continue until the cutting bit is beyond the other end of the core tube. Check the cut and note any points where the core tube wall has been penetrated. Push the router back along the length of the core to the start position. Lower the cutting bit  $\frac{1}{4}$  of a turn on the depth adjuster and repeat cutting process until tube wall is penetrated along its entire length. Once one side of the core tube has been cut to the point where only a sharp knife is required to separate the two halves rotate the core  $180^\circ$  and repeat cutting process until the second side of the core tube has been cut.

### **A2.2.3) Splitting the sediment**

Remove the two inserts that are holding the tube into the plastic bed. Keeping the core tube horizontal carefully remove it from the plastic bed, ensuring that the two halves stay

together, and place on bench surface. Ensure that the two halves of the core tube are completely separated using a sharp knife. With the cuts in the core tube lined up horizontally, place cheese wire across sediment at one end of the tube and move slowly and smoothly through the sediment through the cuts in the tube wall. Rotate the core tube so that the cuts in the core tube are lined up near horizontal and separate the sediment into the two separate halves of the core tube. A pallet knife may be necessary to prise apart sticky sediments, be sure not to smear sediment up or down the core. The core splitting protocol was developed by J.J. Williams and W.D. Gosling.

**A2.3) Photographic set up**

Photographs of each core section were taken and overlapped together to provide one image per core drive (c. 1 m). To ensure maximum clarity and detail of core photographs, several methodologies of photography were tested prior to two methods being utilised. The method used for composite photographs are described below (Table A2.1). Tests were conducted on the different methodologies in order to select those which maximise colour details recorded, consistency between photographs and minimise any limitations of the camera. The full protocol for the photographic setup has already been described in Chapter 3.

Method	Resolution (megapixel)	Optical zoom	Background sheet colour	Lighting	Exposure (seconds)
1	6.1	3x	None	Fluorescent & Spot	1
2	6.1	3x	None	Fluorescent	1
3	6.1	3x	None	None	2
4	6.1	3x	Black	Spot	1
5	6.1	3x	White	None	2
6	6.1	3x	Black	Fluorescent	3

**Table A2.1** Photographic methodologies tested during core cataloguing. Photographs were taken of all cores using both methods 5 and 6. Method 6 was chosen for final publications.



## **A2.4) Fossil pollen and spore analysis**

### **A2.4.1) Sample set up**

#### *Measure*

A typical sample size of 1 cm<sup>3</sup> is measured (maybe reduced to 0.5 cm<sup>3</sup> when using material from smaller diameter tubes) using a water displacement method in a small (c. 5 cm<sup>3</sup>) measuring cylinder. Samples are then transferred to 15 ml plastic centrifuge tubes labelled appropriately. The tubes are centrifuged at 3,000 rpm for 3 minutes, ensuring first that tubes are balanced. Decant off the supernatant in one fluid movement from tubes into a waste container; the solid pellet should be left in the bottom of the tubes. This applies for all centrifuge use throughout the schedule.

#### *Spike*

As *Lycopodium* is a possible component of the natural aquatic taxa, a spike suspension of polystyrene microspheres are used to enable the calculation of fossil pollen concentration during identification. 0.5 cm<sup>3</sup> (or half the quantity of sediment) is added to each tube using a glass pipette. Check the manufactures information for the number of microspheres per cm<sup>3</sup>. It is important that the spike suspension is thoroughly mixed prior to use. This is achieved by using a stir plate for 2 hours at a medium speed setting. The magnetic slug should remain in the solution, which should be stored at 3°C (refer to manufacturer notes).

### **A2.4.2) Solution and removal of carbonates and humic compounds**

#### *HCL Treatment*

To remove carbonates from the samples a hydrochloric acid treatment is used which acidifies the samples to c. pH 1. First, add 1 ml of 10% HCL and stir using a wooden stick. Once any violent reactions have occurred a further 6 ml of 10% HCL can be added to each tube. The tubes are then placed in the water bath (inside the fume cupboard) for 30 minutes at 90°C. Once complete, balance, centrifuge and carefully decant off the yellow/brown coloured supernatant. Unless noted to the contrary, all chemicals may be discarded into the fume cupboard sink with water running continuously.

### *H<sub>2</sub>O Wash*

Whirlimix the sample until fully mobilised and top up with distilled or deionized (DI) water. Balance and centrifuge tubes and decant off supernatant as before.

### *KOH Treatment*

To deflocculate the sediments and remove humic acids a potassium hydroxide procedure is performed which bringing the samples up to pH 14 (alkaline). First, mobilise the sample on the whirlimix and top up the tube with 7 ml of 10% KOH. The tubes are then placed in the water bath in fume cupboard for 10 minutes

### *Sieving*

Label up a second batch of corresponding tubes in a rack with funnels and 180 µm sieves. Using a little DI water washout the contents from the original sample tubes ensuring all material is removed. Using a washbottle with restricting nozzle, wash the material through sieve thoroughly working across the sieve mesh surface. The original tube can also be used to catch material being washed through once the 2<sup>nd</sup> one is full. Centrifuge, decant, whirlimix and refill tubes as necessary (at least 3 times each – equates to c. 90 ml of water being washed through each sieve) as any extra washing here will help towards the next step. From this step onwards each sample is split between two tubes. This particularly aids the following steps of washing.

### *H<sub>2</sub>O Washes*

This step removes any remaining organic acids and fine clay particles. Follow the washing procedure as previously described, and repeat until liquid is clear (usually 6-10 times). Record the total number of washes. The addition of 4% sodium pyrophosphate (Na<sub>4</sub>P<sub>2</sub>O<sub>7</sub>) may help to break up the electrostatic bonds of any clay rich samples (heat for 5 minutes in water bath).

### *HCL Wash*

To assist the action of HF on samples and to make sure there is no residual carbonate, samples are acidified prior to HF treatment. This is achieved by washing in HCL following the same procedure as previously described except using HCL instead of H<sub>2</sub>O.

### **A2.4.3) Solution and removal of silicates and sulphides**

#### *HF Treatment*

To removed silicates from the samples a hydrofluoric acid treatment is used. Samples are first thoroughly mobilised using the whirlimix before 5 ml of HF is added to each tube and stirred with wooden sticks. Avoid drips were possible and dip lower parts of tube into the saturated Sodium Carbonate solution to remove drips of HF from the tube.

Prior to January 2010 and the construction of the new laboratories and backwash fume cupboards, HF treatment was conducted cold during a period of 1 - 2 days depending upon the sample. Once the new labs were operational, samples were placed into a hot water bath at 80°C for 3 hours, with particularly silicate rich samples left overnight. Once complete, tubes are centrifuged and carefully decanted into a labelled collector vessel, not down the sink. The solution is then either disposed of into a waste HF container or neutralised with sodium carbonate before being emptied into the sinks connected to marble chip traps.

#### *HCL Treatment*

To remove siliceous colloidal clumps and fluorosilicate that form during silica digestion, a hot HCL treatment is needed. Follow the procedure as outlined previously.

Examine the sediment packed in the bottom of the tubes at this point. If a small separate gray layer or area is present then there are still silicates in the sample. If unsure, it may also be worthwhile making up a quick slide of material to examine under a microscope. If remaining crystalline materials inhibit pollen counting then the HF treatment needs to be repeated. Two hot HF treatments are generally enough for even very silicate rich samples.

#### *HNO<sub>3</sub> Treatment*

If samples are known to contain sulphides (appear as tiny black cubes about 1–4µm on a side that collect within pollen grains) then a wash in 10% Nitric Acid may be required. To do this, follow the washing procedure as outlined previously but use 10% HNO<sub>3</sub> instead of H<sub>2</sub>O.

#### *H<sub>2</sub>O Wash*

Follow the procedure as previously described.

### **A2.4.4) Removal of cellulose and polysaccharides - acetylation**

#### *CH<sub>3</sub>COOH Wash*

Removal of water is essential before acetolysis can be conducted. This is achieved by washing in Concentrated (glacial) Acetic acid. Follow the washing procedure as previously described except using CH<sub>3</sub>COOH and decanting into a waste beaker.

#### *Acetolysis Treatment*

To remove some organic matter and clean the surface of the grains acetolysis is used. It is important that the mixture is prepared fresh just before use. Using a graduated measuring cylinder mix acetic anhydride and concentrated sulphuric acid (H<sub>2</sub>SO<sub>4</sub>) in a proportion of 9:1. Carefully pour out the acetic anhydride amount required before slowly adding the H<sub>2</sub>SO<sub>4</sub> stirring to prevent heat build-up. Remember, volumetric measurements are made with the bottom of the meniscus touching the required gradation line. Make sure the waterbath is preheated (80 - 90°C) before adding 5 ml of the mixture to each tube. Put samples into water bath and heat for exactly 3 minutes and stir once.

#### *CH<sub>3</sub>COOH Wash*

Remove from water bath and cool immediately by adding 3 ml glacial acetic which neutralises the reaction. Centrifuge and decant into the beaker containing the waste acetic acid. Empty beaker contents down the sink with plenty of water.

#### *H<sub>2</sub>O Wash*

Follow the procedure as previously described.

### **A2.4.5) Slide preparation**

#### *Transfer to microtubes*

Whirlmix remaining material in tubes with a small amount of DI water. Then carefully transfer into appropriately labelled microtubes; centrifuging, decanting and repeating until all residue is transferred.

### *Slide mounting*

To preserve the material until ready to count, it is imperative not to let it dry out. Add equal quantity of glycerol to each sample residue and stir well. With caps left open, any unwanted excess H<sub>2</sub>O will evaporate off. When ready, place a small amount of a sample onto a slide using a cocktail stick cover with coverslip.

This protocol was developed with guidance from W.D. Gosling.

## **A2.5) Charcoal analysis**

### **A2.5.1) Sample set up**

#### *Measure*

A typical sample size of 1 cm<sup>3</sup> is measured using a water displacement method in a small (c. 5 cm<sup>3</sup>) measuring cylinder. Samples are then transferred to 15 ml plastic centrifuge tubes labelled appropriately. The tubes are centrifuged at 3,000 rpm for 3 minutes, ensuring first that tubes are balanced. Decant off the supernatant in one fluid movement from tubes into a waste container; the solid pellet should be left in the bottom of the tubes. This applies for all centrifuge use throughout the schedule.

### **A2.5.2) Wet lab preparation**

#### *KOH Treatment*

To deflocculate the sediments prior to sieving, a potassium hydroxide procedure is performed. First, mobilise the sample on the whirlimix and top up the tube with 7 ml of 10% KOH. The tubes are then placed in the water bath (75°C) in fume cupboard for 5 minutes. They are then removed from the bath and left for 24 hours.

#### *Sieving*

Nest an 180 µm and 100 µm sieve together in a large sink with the 180 µm mesh on top and the 100 µm underneath. Using a cold tap with hose attachment, wash sediments through thoroughly. Wash sievings into two labelled sample tubes, keeping the two size fractions separate as a distinction will be made between the two size fractions when counting.

## **A2.6) Subfossil chironomid analysis**

### **A2.6.1) Sample set up**

#### *Measure*

A typical sample size of 1 g of wet sediment is used for chironomid analysis but the amount of sediment required to obtain substantial numbers of head capsules for analysis varies greatly with each lake and, often, each depth. However, the low sediment budget available for the Bolivian samples results in only 1 g being used for all samples. Samples are placed into 50 ml sample tubes.

### **A2.6.2) Wet lab preparation**

#### *KOH Treatment*

To deflocculate the sediments a potassium hydroxide procedure is performed. 10 ml of 10% KOH is added and samples are placed in a water bath at 75°C for 5 minutes, do not keep in for longer than this time. Mobilise the samples gently periodically.

#### *H<sub>2</sub>O Treatment*

To dilute the KOH and further deflocculate the sample, top up each sample tube with water and continue in water bath for 15 minutes.

#### *Sieving*

Nest a 212 µm and 90 µm sieves together in a large sink with the 212 µm mesh on top and the 90 µm underneath. Using a cold tap with hose attachment, wash sediments through thoroughly but do not use excess pressure, as this will damage the head capsules. Wash sieving into two labelled Petri dishes, keeping the two size fractions separate as this will aid picking.

### **A2.6.3) Picking and mounting procedure**

#### *Picking*

Pipette a small amount into a grooved Perspex sorting tray. Pick out head capsules using fine forceps under a ×25 binocular microscope; do not actually touch the head capsules with the forceps as this will damage them, but instead trap them in a bubble of liquid just behind the tip (practice). Place head capsules into 80% ethanol in a wide necked screw lid

vial which can then be labelled and stored in the fridge until ready to mount up. Allow the forceps to dry after placing in the ethanol as if placed directly into the sorting tray this will cause the sample to rapidly disperse.

### *Dehydrating*

Progressively dehydrate head capsules by passing through 90% ethanol and Euparal Essence (about 5 minutes in each). Use the staining blocks to do this but remember to cover them with the glass covers to prevent excess evaporation. Do not use too much Euparal Essence and remember not to try and process too many head capsules at once. Depending on size and the ease of picking, 10–20 at a time is about right.

### *Mounting*

Using a slide template (see Figure A2.3), arrange six drops of Euparal mountant evenly spaced on each side. Carefully place into each drop two head capsules, ventral side up. Once checked for appropriate positioning, cover each drop with a 6 mm diameter coverslip and store slides flat.

As a rule, it is best to do as little chemical steps to the samples as possible. Do not bring samples to the boil and avoid stirring samples too vigorously with wooden sticks, as this will begin to damage and disintegrate the head capsules.

This protocol was developed with guidance from S.J. Brooks

## **A2.7) Elemental determination**

### **A2.7.1) Instrumentation**

The abundance (wt%) of total carbon (TC), total inorganic carbon (TIC), Sulphur (S) and Nitrogen (N) was determined using the in-house LECO CNS-2000 elemental analyzer. The LECO CNS-2000 comprises of an auto-sampler, capable of holding 49 samples, and a furnace kept at 1350°C. Samples are weighed into inert ceramic boats, which have been preconditioned by placing them in a separate furnace for 1 hr at 1000°C, and then stored in a desiccator before use. The auto-sampler introduces boats into the furnace in turn for



combustion. CO<sub>2</sub> and SO<sub>2</sub> gases are then analysed and abundance of C and S determined via the use of infrared detector cells, and processed by the LECO CNS-2000 computer system. TOC is calculated as by the subtraction of TIC from TC. All TIC is assumed to be in the form of CaCO<sub>3</sub>, which is obtained by multiplying the TIC values by 8.33.

**A2.7.2) Measurement protocol**

*TC, S and N*

For TC, S and N, 0.2 g of dried, finely ground sediment samples were weighed into the boats. 1 g of the combustion catalyst ComCat is added to the sample and mixed with the sample thoroughly to ensure, a rapid, complete combustion.

*TIC*

Measurements for TIC were established using sample weights of 0.15 g. These sample were first “ashed” at 450°C to remove all organic carbon and then mixed with ComCat and run as per the TC, S and N measurement.

*Standards*

The auto-sampler accepts a total of 49 boats. 40 sediment samples are loaded, with the remaining 9 spaces occupied with a range of other readings. Two empty boats (blanks) and 2 pure ComCat (1.0 g) are measured at the start of run, and intermittent standards of known values are measured every 10 samples to allow for any long-term drift to be assessed. The standard used for all analysis was The Open University’s in house Oxford Clay (OX-12g). The reproducibility of these standards is shown in Table A2.2.

This protocol was established with guidance from A.L. Coe.

Dates	Number run	Carbon (wt%)	Sulphur (wt%)	Nitrogen (wt%)
8 – 15 <sup>th</sup> Oct 09	45	4.475 ± 0.179	1.213 ± 0.092	0.116 ± 0.067

**Table A2.2** Mean values for in house Oxford Clay standard (OX-12g). Uncertainties calculated as 2 standard deviation.

<b>Fossil Pollen Preparation Tick Sheet – Andean Sediments</b>												
Date :												
Worker:												
Sheet No:												
Sediment Quantity												
Microspheres Quantity												
Hot 10% HCl (30mins)												
In:												
Out:												
H <sub>2</sub> O Wash												
Hot 10% KOH (10mins)												
Sieve x3												
H <sub>2</sub> O Wash (until clear)												
Add Na <sub>2</sub> P <sub>2</sub> O <sub>7</sub> to clay rich samples												
10% HCL Wash												
HF												
In:												
Out:												
Hot 10% HCl (30mins)												
In:												
Out:												
10% HNO <sub>3</sub> Wash												
H <sub>2</sub> O Wash												
CH <sub>3</sub> COOH Wash												
Acetolysis (3mins)												
9 parts Acetic Anhydride												
1 part Sulphuric Acid												
CH <sub>3</sub> COOH Wash												
H <sub>2</sub> O Wash												
Vial												

Version 1.1 – Joseph J Williams

Figure A2.1 Fossil pollen preparation tick sheet for Andean lake sediments.

**Pollen Count Sheet – Eastern Bolivia Cordillera (Cochabamba Basin)**

<b>Sample Code:</b>	<b>Analyst:</b>	
<b>Relative Depth:</b>	<b>Date:</b>	<b>Sheet #: POL</b>
<b>Sediment Quantity:</b>	<b>Microsphere Quantity:</b>	

<b>Pollen</b>	<b>Spores</b>
<i>Alnus</i>	Monolete
Amaranthaceae	
Anacardiaceae	
Apiaceae	Trilete (cf Lyco)
Araceae	
Asteraceae	
Brassicaceae	
Bromeliaceae	<i>Sporomiella</i>
Caryophyllaceae	<i>SpyraG</i> (HHT 374-5)
Chloranthaceae (cf <i>Hedyosmum</i> )	Other
Chenopodiaceae	
Compositae	
Ericaceae	
Euphorbiaceae (cf <i>Acalypha</i> )	
Euphorbiaceae (others)	
Fabaceae	<b>Non-Pollen</b>
Flacourtiaceae	Microspheres
Gunneraceae	<i>Pediastrum</i> (Simplex)
Juglandaceae	(Duplex)
Loganiaceae	Chironomid Parts
Melas / Comb	
Mora / Urti	
Onagraceae (cf <i>Ludwigia</i> )	<b>Unknown Types</b>
Papaveraceae	
Piperaceae	
Poaceae	
Podocarpus	
Ranunculaceae	
Rosaceae (cf <i>Polylepis</i> )	
Rubiaceae	
Solanaceae	
Ulmaceae (cf <i>Trema</i> )	
(cf <i>Celtis</i> )	
Cyperaceae	
<i>Isoetes</i>	<b>Damaged Grains</b>
<i>Myriophyllum</i>	Broken
Typhaceae	Crumpled
	Corroded
	Obscured
	Degraded

Created by JJW. Version 1 (March 2009)

**Figure A2.2** Fossil pollen count sheet for Andean lake sediments.

<b><u>Chironomid Slide Count Sheet</u></b>	
<b>Site and Depth:</b>  <b>Short Code:</b> <b>Relative Depth:</b> cm	<b>Date:</b> /      / <b>Analyst:</b> <b>Sheet number:</b> CHIRON <b>Slide Number:</b>
i)	vi)
ii)	vii)
iii)	viii)
iv)	ix)
v)	x)

**Slide Layout**

	V	IV	III	II	I
	VI	VII	VIII	IX	X

Created by JJW. Version 1. May 2009

**Figure A2.3** Subfossil chironomid count sheet for Andean lake sediments

## **Appendix A3) Bolivian lake sediment data**

This appendix presents the data collected from the sediments of Lake Challacaba and Laguna Khomer Kocha Upper which have been discussed in this thesis (Chapters 4–6). Data is presented here in tabulated form, with large data sets on compact disc (Enclosure CD1). Sample codes refer to lake, core site, drive, drive depth.

---

### **A3.1) Radiometric dates**

A chronological framework for all cores was established using radiocarbon dating ( $^{14}\text{C}$ ) of either plant macrofossils, Lake sediments (gyttja) or macroscopic charcoal and seed cases (see Chapter 3). All dates were obtained via the Scottish Universities Environmental Research Centre (SUERC) Radiocarbon Facility (Environment) administered by the Natural Environment Research Council (NERC). Two rounds of funding were awarded by the NERC Radiocarbon Facility-Steering Committee (RCF-SC), reference numbers 1287.0408/2008 and 1463.0410/2010.

#### **A3.1.1) Sample pre-treatment and analysis**

All chemical pre-treatment and analysis was conducted at the SUERC Facility, East Kilbride. Samples were digested in 1M HCl (80°C, 30 mins), washed free from mineral acid with deionised water then digested in 0.2M KOH (80°C, 20 mins). The digestion was repeated using deionised water until no further humics were extracted. The residue was rinsed free of alkali, digested in 1M HCl (80°C, 1 hour) then rinsed free of acid, dried and homogenised. The total carbon in a known weight of the pre-treated sample was recovered as  $\text{CO}_2$  by heating with CuO in a sealed quartz tube. The gas was converted to graphite by Fe/Zn reduction. Sample graphite's were analysed using Accelerator Mass Spectrometry (AMS). See Freeman et al. (2007) for facility information.

While all samples were pre-treated and prepared to  $\text{CO}_2$  identically, SUERC-32100, -32101 and -32102 contained <500  $\mu\text{gC}$  and required analysis at low current and preparation of additional standards which matched the sample carbon weights.  $^{13}\text{C}/^{12}\text{C}$  ratios for samples <500  $\mu\text{gC}$  were measured on the SUERC AMS during  $^{14}\text{C}$  determination and used to model  $\delta^{13}\text{C}$  values by comparison to the Craig (1957)  $^{13}\text{C}/^{12}\text{C}$  value for PDB standard.

These  $^{13}\text{C}$  values are shown in brackets and were considered the most appropriate to normalise  $^{14}\text{C}$  data to  $\delta^{13}_{\text{CVPDB}}\text{‰} = -25$ , but are not necessarily representative of the  $\delta^{13}\text{C}$  in the original sample material. The  $\delta^{13}\text{C}$  values not in brackets were measured on a dual inlet stable isotope mass spectrometer (VG OPTIMA) and are representative of  $\delta^{13}\text{C}$  in the original, pre-treated sample material.

### **A3.1.2) Reported results**

Original results reported by the SUERC AMS Laboratory, together with calibration calculations, are given in Table A3.1. The position of each date is marked on the initial core description (Appendix 1).

For reference purposes, a complete list of all depths (per cm) and associated ages (cal yr BP) is provided in a spreadsheet file on Enclosure CD1. The data is divided by study site into the following files:

- Lake Challacaba Depth vs Age Data.xls
- Laguna Khomer Kocha Upper Depth vs Age Data.xls

Publication code	Sample code (type)	Depth (cm blf)	<sup>14</sup> C	Conventional	Carbon	$\delta^{13}\text{C}_{\text{VPDB}}\text{‰}$ ± 0.1	Calibrated dates	
			Enrichment (% Modern ± 1σ)	Radiocarbon Age (years BP ± 1σ)	content (% by wt.)		Range (cal yr BP)	Curve used
SUERC 21929	V2B 3 52 cm (MF)	197	74.79 ± 0.35	2333.19 ± 37.75	16	-21.8	2155 - 2270	SHcal04
SUERC 21930	V2B 4 39 cm (MF)	284	63.79 ± 0.29	3611.33 ± 36.96	30	-14	3616 - 3933	SHcal04
SUERC 22351	V2B 1 45 cm (BS)	91	88.49 ± 0.40	982 ± 37	3.2	-24.2	770 - 925	SHcal04
SUERC 22352	V2B 3 52 cm (BS)	197	72.24 ± 0.31	2,612 ± 35	6.1	-24.3	2490 - 2643	SHcal04
SUERC 22355	V2B 4 39 cm (BS)	284	57.31 ± 0.25	4471 ± 36	4.2	-27.2	4864 - 5071	SHcal04
SUERC 22356	KKUA 1 30.5cm (BS)	61.5	84.43 ± 0.38	1359 ± 37	9.6	-24.6	1148 - 1300	SHcal04
SUERC 22357	KKUA 4 13 cm (BS)	321	36.54 ± 0.18	8086 ± 41	13.5	-24.5	8661 - 9029	SHcal04
SUERC 22358	KKUA 5 37.5 cm (BS)	445.5	17.26 ± 0.13	14112 ± 61	7.6	-24.2	16363 - 16645	FairB
SUERC 32100	V2B-4-20 cm (CHAR)	265	63.56 ± 0.73	3640 ± 92	N/A	(-27.6)	3639-4102	SHcal04
SUERC 32101	KKUA-2-15 cm (CHAR)	123	67.79 ± 0.75	3123 ± 89	N/A	(-35.8)	2998 - 3461	SHcal04
SUERC 32102	KKUA-4-85 cm (CHAR)	385	33.74 ± 0.53	8727 ± 125	N/A	(-21.0)	9472 - 10153	SHcal04
SUERC 31725	KKUB-2-70 cm (CHAR)	210	47.92 ± 0.23	5910 ± 38	N/A	-24.6	6545 - 6783	SHcal04
SUERC 31726	KKUA-3-55 cm (CHAR)	263	46.28 ± 0.22	6190 ± 38	N/A	-25.2	6906 - 7162	SHcal04
SUERC 31727	KKUA-4-55 cm (CHAR)	358	35.14 ± 0.17	8400 ± 40	N/A	-24.4	9149 - 9479	SHcal04

**Table A3.1** Full listing of radiocarbon dates and calibration calculations obtained for Lake Challacaba and Laguna Khomer Kocha Upper. Sample type: MF = plant macrofossils. BS = lake sediments (gyttja). CHAR = macroscopic charcoal and seed cases. N/A = pre-treatment method precluded %C determination. Calibrations: SHcal04 = Software CALIB 6.01 and the SHCal04 Southern Hemisphere data set (McCormac et al., 2004; Stuiver and Reimer, 1993; Stuiver et al., 2005). FairB = Fairbanks Calibration Curve (Fairbanks et al., 2005).



### A3.2) Geochemical and physical data

All non-ecological data obtained from the sediments of both study sites is presented in Table A3.2 (Lake Challacaba) and Table 3A.3 (Laguna Khomer Kocha Upper). Magnetic susceptibility values are given in both initial corrected susceptibility ( $\kappa$ ) and mass specific susceptibility value ( $\chi$ ). Colour intensity values are provided for the colour channels red (R), green (G) and blue (B), and an averaged value of the 3 is also given (mean RGB). The abundances of total carbon (TC), calcium carbonate ( $\text{CaCO}_3$ ), total organic carbon (TOC), Sulphur (S) and Nitrogen (N) are given as weight percent (wt%). Depth are provided in centimetres below the lake floor (cm blf). Detailed analytical methodologies are described in Chapter 3 and Appendix A2.

**Table A3.2** Full listing of Lake Challacaba geochemical and physical data. V2B = core site B. V2C = core site C. SS = Sediments from short core (sediment/water interface).

Sample code	Depth (cm blf)	Magnetic susceptibility value		Colour intensity				Elemental (wt%)				
		$\kappa$	$\chi$	Red	Green	Blue	Mean RGB	TC	$\text{CaCO}_3$	TOC	S	N
V2B SS 1cm	1	4.250	29.720	151.066	122.667	109.516	127.752	2.983	0.241	2.954	0.154	0.443
V2B SS 5cm	5	4.500	25.714	150.201	121.306	107.737	126.419	3.831	0.290	3.796	0.260	0.559
V2B SS 10cm	10	3.900	26.174	159.930	131.981	117.761	136.556	2.570	0.242	2.541	0.145	0.365
V2B SS 15cm	15	5.350	29.076	156.296	128.842	115.594	133.576	1.921	0.193	1.898	0.097	0.283
V2B SS 20cm	20	5.500	27.228	169.994	144.583	128.181	147.586	1.352	0.290	1.317	0.057	0.237
V2C SS 25cm	25	5.800	29.442	166.600	141.155	125.836	144.534	1.205	0.242	1.176	0.048	0.232
V2C SS 30cm	30	8.700	33.721	162.714	135.242	120.488	139.479	1.423	0.290	1.388	0.064	0.245
V2C SS 35cm	35	6.600	33.000	164.672	137.129	121.376	141.058	1.440	0.242	1.411	0.070	0.241
V2C SS 40cm	40	8.650	34.600	164.952	138.019	121.021	141.328	1.034	0.242	1.005	0.036	0.191
V2C SS 45cm	45	8.550	32.264	160.790	134.989	120.944	138.909	1.044	0.242	1.015	0.043	0.193

Appendix A3) Bolivian lake sediment data

V2C SS 50cm	50	8.200	41.837	148.702	120.720	109.956	126.462	2.609	0.289	2.574	0.131	0.341
V2B 1 5cm	51	3.350	24.632	158.829	133.320	120.343	137.497	1.858	0.391	1.811	0.062	0.255
V2C SS 55cm	55	8.700	40.465	155.735	127.377	115.627	132.916	2.258	0.289	2.223	0.106	0.279
V2B 1 10cm	56	4.050	29.348	170.033	144.967	129.928	148.316	1.285	0.381	1.239	0.049	0.212
V2C SS 60cm	60	5.350	34.516	139.271	109.410	100.368	116.354	3.788	0.290	3.753	0.228	0.442
V2B 1 15cm	61	4.200	26.752	167.686	141.921	126.627	145.414	1.197	0.399	1.149	0.108	0.204
V2B 1 20cm	66	4.700	29.375	161.124	132.976	118.081	137.392	1.587	0.503	1.527	0.151	0.237
V2B 1 25cm	71	5.350	29.558	161.404	133.367	118.483	137.751	1.666	0.444	1.613	0.050	0.242
V2B 1 30cm	76	5.500	41.045	162.832	135.480	119.281	139.197	1.125	0.393	1.078	0.040	0.184
V2B 1 35cm	81	4.350	31.752	157.370	132.498	121.075	136.980	1.840	0.448	1.786	0.069	0.259
V2B 1 40cm	86	4.450	36.179	155.489	128.041	116.965	133.498	2.220	0.511	2.159	0.140	0.275
V2B 1 45cm	91	4.800	37.209	146.447	118.460	110.089	125.000	3.169	0.443	3.116	0.088	0.382
V2B 1 50cm	96	3.550	29.098	140.116	111.508	104.127	118.580	3.607	0.681	3.525	0.131	0.414
V2C 1 70cm	97	3.450	30.000	141.703	113.072	103.379	119.389	3.787	0.338	3.746	0.150	0.427
V2B 2 40cm	100	4.200	36.522	145.357	117.573	107.067	123.336	2.895	0.508	2.834	0.059	0.146
V2C 1 75cm	103	3.000	29.412	134.753	106.609	99.293	113.551	5.135	0.338	5.094	0.202	0.588
V2B 2 45cm	105	3.100	31.633	138.001	108.745	98.899	115.215	3.690	0.452	3.636	0.154	0.341
V2C 2 5cm	108	0.800	9.524	124.083	94.307	90.495	102.962	8.591	0.387	8.545	0.377	0.784
V2B 2 50cm	110	3.400	31.193	134.408	105.642	97.939	112.664	4.126	0.501	4.066	0.178	0.415
V2C 2 10cm	113	0.800	10.811	122.667	93.591	90.335	102.199	9.246	0.387	9.200	0.679	0.958
V2B 2 55cm	115	1.700	18.085	128.356	99.163	93.347	106.944	6.284	0.502	6.224	0.493	0.459
V2B 2 60cm	120	0.750	9.036	124.930	96.053	92.881	104.624	7.727	0.510	7.666	0.557	0.661
V2B 2 65cm	125	0.950	12.025	102.919	72.875	70.776	82.192	10.920	0.513	10.858	0.644	0.733

Appendix A3) Bolivian lake sediment data

V2B 2 70cm	130	0.400	5.797	109.251	78.956	77.242	88.479	12.750	5.335	12.110	0.802	1.057
V2B 2 75cm	135	0.350	6.034	97.206	66.631	65.105	76.315	21.580	11.66 2	20.180	1.707	1.083
V2B 2 80cm	140	1.400	14.000	98.791	68.153	64.981	77.311	16.810	6.482	16.032	1.145	1.989
V2B 2 85cm	145	0.750	9.375	102.585	72.329	70.375	81.764	16.060	5.427	15.409	2.082	1.535
V2B 2 90cm	150	0.800	8.163	104.149	74.873	73.020	84.015	15.580	6.317	14.822	1.262	1.518
V2B 2 95cm	155	1.200	10.084	102.724	73.306	71.712	82.577	17.570	5.537	16.905	1.283	0.147
V2B 3 30cm	175	1.350	13.500	120.612	93.046	89.295	100.978	12.840	3.310	12.443	1.319	1.418
V2B 3 35cm	180	1.950	15.984	124.927	98.049	93.969	105.644	11.760	3.132	11.384	0.895	1.614
V2B 3 40cm	185	2.150	19.027	118.451	90.207	86.100	98.249	13.070	0.798	12.974	1.009	1.139
V2B 3 45cm	190	2.550	19.318	119.166	92.864	91.256	101.099	10.290	0.457	10.235	0.739	1.063
V2C 2 90cm	193	0.600	6.977	128.684	103.193	100.157	110.682	8.640	0.436	8.588	1.050	0.886
V2B 3 52cm	197	1.050	10.714	124.886	99.322	98.085	107.428	7.227	0.456	7.172	0.776	1.190
V2C 2 95cm	198	1.250	11.161	136.440	111.187	107.017	118.217	5.888	0.388	5.841	0.790	0.577
V2B 3 55cm	200	0.900	8.911	126.558	101.095	99.414	109.021	8.049	0.456	7.994	1.255	1.008
V2B 3 60cm	205	1.000	9.174	127.058	102.687	101.753	110.505	7.325	0.399	7.277	1.282	0.750
V2C 3 5cm	208	0.650	9.155	105.717	77.622	75.749	86.360	12.590	0.436	12.538	2.696	1.369
V2B 3 65cm	210	0.850	11.184	92.209	65.510	65.540	74.412	16.200	0.342	16.159	3.050	0.782
V2C 3 10cm	213	0.800	9.524	121.313	92.436	90.009	101.251	9.230	1.401	9.062	1.475	1.001
V2B 3 70cm	215	0.350	5.072	82.817	58.253	59.215	66.762	16.640	0.457	16.585	3.163	0.751
V2C 3 15cm	218	0.350	4.268	134.692	107.536	103.730	115.319	8.917	0.434	8.865	1.774	0.963
V2B 3 75cm	220	0.550	6.627	99.044	73.272	74.663	82.328	11.600	0.456	11.545	2.293	1.752
V2B 3 80cm	225	0.150	2.381	85.759	59.707	63.220	69.562	22.640	0.457	22.585	3.335	0.180
V2B 3 85cm	230	0.100	1.852	88.285	61.964	66.041	72.098	27.070	0.457	27.015	2.338	1.771

Appendix A3) Bolivian lake sediment data

V2B 3 90cm	235	0.350	4.487	107.272	80.228	80.738	89.417	13.920	0.457	13.865	1.813	1.205
V2B 3 95cm	240	0.400	5.000	105.388	78.655	79.072	87.713	15.670	0.513	15.608	2.666	2.257
V2B 3 99cm	244	0.500	5.263	109.272	82.244	82.292	91.270	14.520	0.572	14.451	2.239	2.501
V2B 4 3cm	248	0.950	13.380	97.318	69.303	68.360	78.323	22.430	0.629	22.355	2.147	1.429
V2B 4 10cm	255	0.100	1.266	104.955	75.474	73.833	84.756	16.970	2.226	16.703	1.919	1.573
V2B 4 15cm	260	0.400	3.704	109.164	80.589	79.682	89.814	12.290	5.192	11.667	2.692	1.478
V2B 4 20cm	265	0.400	3.077	118.073	91.238	89.796	99.710	8.644	8.024	7.681	1.189	0.628
V2B 4 25cm	270	0.200	1.852	119.990	93.500	91.933	101.812	8.290	7.007	7.449	1.398	0.621
V2C 3 70cm	273	0.650	5.118	124.165	99.433	98.863	107.494	8.672	10.67 9	7.390	0.848	0.603
V2B 4 30cm	275	0.950	6.884	125.947	100.336	98.740	108.340	8.581	9.171	7.480	0.731	0.600
V2C 3 75cm	278	0.650	4.643	127.695	103.291	102.670	111.222	8.549	10.45 4	7.294	0.581	0.581
V2B 4 35cm	280	1.150	6.886	132.388	108.456	107.247	116.036	6.070	7.485	5.171	1.601	0.213
V2B 4 39cm	284	1.150	6.725	142.126	119.510	117.625	126.423	4.705	8.273	3.712	0.241	0.315
V2B 4 45cm	290	1.500	7.979	147.838	127.609	126.304	133.914	3.129	17.28 5	1.054	0.122	0.132
V2B 4 50cm	295	1.900	9.645	177.140	164.289	159.119	166.847	0.164	0.241	0.135	0.441	0.092



**Table A3.3** Full listing of Laguna Khomer Kocha Upper geochemical and physical data. KKUA = core site A.  
KKUB = core site B.

Sample code	Depth (cm blf)	Magnetic susceptibility value		Colour intensity				Elemental (wt%)				
		$\kappa$	$\chi$	Red	Green	Blue	Mean RGB	TC	CaCO <sub>3</sub>	TOC	S	N
KKUA 1 20cm	43	-0.300	-7.143	132.724	108.776	108.918	116.803	11.040	1.839	10.819	0.326	0.758
KKUA 1 25cm	51	-0.200	-4.255	130.648	107.332	108.090	115.352	11.170	0.630	11.094	0.304	0.754
KKUA 1 30.5cm	61.5	-0.050	-1.163	107.836	81.791	87.501	92.384	12.850	0.627	12.775	0.354	0.858
KKUA 1 35cm	66	-0.150	-2.500	132.783	109.717	111.051	117.847	9.118	0.582	9.048	0.284	0.719
KKUA 1 40cm	71	-0.250	-5.682	124.526	101.066	104.584	110.059	9.742	0.531	9.678	0.333	0.711
KKUA 1 55cm	77	-0.100	-1.639	127.644	104.353	106.161	112.716	12.110	0.579	12.041	0.371	0.823
KKUA 1 60cm	82	0.050	1.064	106.045	80.222	85.785	90.692	14.320	0.484	14.262	0.521	0.946
KKUA 1 65cm	87	-0.100	-1.786	109.503	83.647	88.944	94.038	14.550	0.678	14.469	0.476	0.967
KKUA 1 85cm	93	0.100	1.724	97.958	71.639	78.130	82.576	17.670	0.774	17.577	0.555	1.135
KKUA 1 90cm	98	-0.150	-3.125	87.185	61.095	67.735	72.004	18.180	0.580	18.110	0.926	1.118
KKUA 1 95cm	103	-0.150	-3.000	110.246	85.377	90.957	95.527	16.160	0.510	16.099	0.707	0.829
KKUA 1 100cm	108	-0.150	-2.830	109.412	84.163	89.745	94.442	14.350	0.463	14.294	0.520	0.774
KKUA 2 5cm	113	0.100	1.887	86.887	61.290	68.828	72.339	15.740	0.698	15.656	0.502	0.816
KKUA 2 10cm	118	-0.150	-3.061	84.810	59.476	65.515	69.934	18.390	0.464	18.334	0.807	1.090
KKUA 2 15cm	123	-0.150	-3.409	86.166	60.322	67.505	71.331	18.680	0.578	18.611	0.722	1.044
KKUA 2 20cm	128	-0.100	-2.000	98.133	72.203	79.588	83.301	16.960	0.696	16.876	0.599	0.904
KKUA 2 25cm	133	-0.250	-5.208	94.188	67.809	74.325	78.770	16.580	0.640	16.503	0.568	0.935
KKUA 2 30cm	138	-0.100	-1.282	119.342	93.940	99.475	104.254	9.157	0.520	9.095	0.243	0.488
KKUA 2 35cm	143	-0.250	-5.435	104.636	79.663	86.192	90.156	15.130	0.637	15.054	0.532	0.821

Appendix A3) Bolivian lake sediment data

KKUA 2 40cm	148	-0.100	-1.961	105.115	79.798	86.729	90.541	15.020	0.464	14.964	0.507	0.814
KKUA 2 45cm	153	-0.150	-2.941	107.026	81.746	88.577	92.443	17.850	0.581	17.780	0.569	0.974
KKUA 2 50cm	158	-0.100	-2.857	117.800	93.779	98.552	103.376	17.930	0.581	17.860	0.586	1.002
KKUA 2 55cm	163	0.250	5.435	112.670	88.084	93.698	98.147	13.230	0.521	13.167	0.422	0.745
KKUA 2 60cm	168	-0.350	-6.140	125.933	103.312	105.863	111.705	11.820	0.463	11.764	0.423	0.660
KKUA 2 65cm	173	-0.250	-5.814	116.117	91.598	96.764	101.492	16.470	0.522	16.407	0.593	0.850
KKUA 2 70cm	178	-0.200	-4.082	102.916	77.528	85.239	88.552	16.370	0.639	16.293	0.560	0.847
KKUA 2 75cm	183	-0.200	-3.333	92.740	67.371	75.044	78.388	15.890	0.579	15.820	0.506	0.839
KKUA 2 80cm	188	-0.300	-6.122	76.809	53.531	61.435	63.928	19.190	0.580	19.120	0.582	1.011
KKUA 2 85cm	193	-0.150	-3.000	97.363	72.362	79.431	83.046	15.710	0.580	15.640	0.432	0.882
KKUA 2 90cm	198	-0.350	-5.833	107.319	82.422	89.873	93.198	13.510	0.463	13.454	0.408	0.767
KKUA 2 95cm	203	-0.200	-3.448	105.363	80.247	87.861	91.148	13.930	0.578	13.861	0.390	0.762
KKUB 2 65cm	205	-0.100	-1.754	73.368	49.194	55.742	59.434	15.060	0.693	14.977	0.316	0.898
KKUA 2 100cm	208	-0.250	-4.808	97.208	72.383	80.668	83.426	16.050	0.511	15.989	0.505	0.878
KKUB 2 70cm	210	0.500	3.704	63.296	40.950	46.829	50.358	14.180	0.581	14.110	0.237	0.759
KKUB 2 75cm	215	-0.150	-4.054	85.990	59.722	63.996	69.899	14.810	0.349	14.768	2.393	1.179
KKUB 2 80cm	220	-0.100	-1.563	66.613	43.635	49.016	53.085	16.440	1.334	16.280	0.551	0.962
KKUB 2 85cm	225	0.050	0.694	59.980	38.930	44.153	47.687	16.310	0.981	16.192	0.293	0.996
KKUB 2 90cm	230	0.200	1.869	75.910	50.632	56.422	60.985	12.510	0.752	12.420	0.200	0.735
KKUA 3 25cm	233	-0.050	-0.746	78.399	53.941	61.643	64.665	16.820	0.464	16.764	0.474	0.929
KKUA 3 30cm	238	0.000	0.000	74.837	50.278	57.391	60.834	15.020	0.464	14.964	0.384	0.867
KKUA 3 35cm	243	0.100	1.064	90.025	64.718	71.161	75.299	12.920	0.349	12.878	0.933	0.888
KKUA 3 40cm	248	-0.100	-1.667	70.669	47.360	54.144	57.391	17.400	0.521	17.337	0.450	1.094

Appendix A3) Bolivian lake sediment data

KKUA 3 45cm	253	-0.050	-0.694	63.261	41.490	47.679	50.811	14.070	0.581	14.000	0.285	0.875
KKUA 3 50cm	258	0.150	1.339	83.747	57.085	64.131	68.324	12.020	0.696	11.936	0.223	0.641
KKUA 3 55cm	263	0.050	0.543	77.909	52.992	60.930	63.945	14.340	0.523	14.277	0.325	0.813
KKUA 3 60cm	268	0.050	0.617	72.044	48.351	55.075	58.489	14.680	0.637	14.604	0.448	0.835
KKUA 3 65cm	273	0.050	0.543	74.557	49.833	55.456	59.947	14.000	0.579	13.930	0.739	0.839
KKUA 3 70cm	278	0.100	0.935	69.362	45.722	51.910	55.663	13.210	0.639	13.133	0.351	0.765
KKUA 3 75cm	283	-0.150	-1.923	79.207	54.221	61.819	65.084	14.380	0.869	14.276	0.267	0.886
KKUA 3 80cm	288	-0.050	-0.602	64.758	42.369	49.027	52.053	14.590	0.929	14.479	0.285	0.841
KKUA 3 85cm	293	-0.250	-3.906	86.567	61.980	69.701	72.754	15.610	0.518	15.548	0.379	1.113
KKUA 3 90cm	298	-0.150	-2.174	78.657	54.434	61.703	64.934	15.240	0.516	15.178	0.361	1.074
KKUA 3 95cm	303	-0.050	-0.595	83.660	58.106	65.213	68.996	15.450	0.575	15.381	0.337	1.010
KKUA 3 100cm	308	-0.050	-0.781	87.443	61.004	67.640	72.027	14.780	0.574	14.711	0.370	0.948
KKUA 4 5cm	313	-0.250	-4.098	94.810	69.250	77.012	80.357	16.110	0.578	16.041	0.391	1.083
KKUA 4 10cm	317	-0.300	-4.762	111.888	87.949	94.025	97.950	13.230	0.345	13.189	0.402	0.878
KKUA 4 13cm	320	0.050	0.581	81.529	55.698	62.144	66.458	12.480	0.518	12.418	0.252	0.762
KKUA 4 20cm	326	-0.200	-2.740	102.163	76.490	83.194	87.277	12.970	0.461	12.915	0.334	0.872
KKUA 4 25cm	331	-0.050	-0.625	82.606	56.384	62.457	67.149	14.640	0.573	14.571	0.547	1.042
KKUA 4 30cm	335	-0.200	-3.279	86.947	61.558	68.733	72.416	17.720	0.403	17.672	0.554	1.304
KKUA 4 35cm	340	0.000	0.000	81.736	56.451	63.117	67.105	13.740	0.573	13.671	0.329	0.956
KKUA 4 40cm	344	-0.100	-1.389	83.791	59.221	66.944	69.990	15.430	0.575	15.361	0.351	1.042
KKUA 4 45cm	349	0.050	0.595	84.090	58.516	65.567	69.392	13.750	0.460	13.695	0.401	0.933
KKUA 4 50cm	353	0.100	1.316	97.645	71.605	78.660	82.633	12.830	0.460	12.775	0.362	0.886
KKUA 4 55cm	358	0.050	0.602	87.401	60.973	67.586	71.985	12.590	0.460	12.535	0.315	0.891



Appendix A3) Bolivian lake sediment data

KKUA 4 60cm	362	-0.050	-0.649	103.363	78.082	82.894	88.120	12.290	0.575	12.221	0.460	0.997
KKUA 4 65cm	367	-0.050	-0.658	100.041	74.483	79.770	84.767	13.030	0.749	12.940	0.598	1.076
KKUA 4 70cm	371	0.200	1.905	92.775	65.969	72.016	76.920	11.870	0.518	11.808	0.666	0.841
KKUA 4 75cm	376	0.100	0.980	81.285	55.475	62.170	66.310	12.760	0.631	12.684	0.424	0.811
KKUA 4 80cm	380	-0.250	-3.378	103.683	78.546	85.252	89.152	11.630	0.803	11.534	0.361	0.838
KKUA 4 85cm	385	0.050	0.532	78.549	54.263	60.558	64.460	12.820	0.517	12.758	0.451	1.010
KKUA 4 90cm	389	0.700	4.965	78.013	52.920	59.391	63.441	11.440	0.517	11.378	0.218	0.646
KKUA 4 95cm	394	0.150	1.546	104.456	78.104	83.553	88.710	9.550	0.345	9.509	0.320	0.734
KKUA 4 100cm	398	-0.150	-2.143	99.494	74.814	82.383	85.564	13.230	0.518	13.168	0.319	1.044
KKUA 4 105cm	403	0.200	2.247	107.973	82.021	87.251	92.422	8.569	0.461	8.514	0.221	0.694
KKUA 4 110cm	407	-0.150	-2.459	102.865	78.232	83.060	88.049	11.740	0.461	11.685	0.293	0.957
KKUA 5 5cm	413	0.100	1.220	118.759	95.002	97.738	103.833	9.259	0.461	9.204	0.234	0.823
KKUA 5 10cm	418	-0.050	-0.649	132.040	107.245	103.379	114.221	8.196	0.459	8.141	0.248	0.690
KKUA 5 15cm	423	0.000	0.000	137.397	113.641	109.464	120.169	9.558	0.402	9.510	0.253	0.772
KKUA 5 20cm	428	0.150	1.667	141.404	116.789	112.427	123.539	6.639	0.403	6.591	0.185	0.551
KKUA 5 25cm	433	0.200	2.128	135.057	110.942	105.868	117.286	6.381	0.518	6.319	0.385	0.534
KKUA 5 30cm	438	0.800	5.926	148.102	125.406	120.833	131.447	3.184	0.403	3.136	0.322	0.284
KKUA 5 35cm	443	0.550	4.741	151.270	128.818	124.249	134.776	3.913	0.403	3.865	0.224	0.367
KKUA 5 37.5cm	445.5	0.000	0.000	134.498	109.175	105.786	116.488	7.673	0.692	7.590	0.414	0.800
KKUA 5 40cm	448	1.850	7.582	146.999	124.595	123.314	131.639	3.090	0.344	3.049	0.416	0.312
KKUA 5 45cm	453	19.35 0	134.37 5	185.302	167.496	167.033	173.282	0.064	0.057	0.057	0.044	0.002
KKUA 5 50cm	458	2.250	9.615	172.738	156.305	157.314	162.118	0.682	0.748	0.592	0.064	0.067

### **A3.3) Ecological proxies data**

#### **A3.3.1) Pollen and spore**

The original data obtained from fossil pollen and spore analysis, including percentage and concentration calculations, is provided as an electronic spreadsheet file in Enclosure CD1. Taxa list provided in Appendix A4. The data is divided by study site into the following files:

- Lake Challacaba Pollen Data.xls
- Laguna Khomer Kocha Upper Pollen Data.xls

A description of the methodology used is provided in Sections 3.4.1, 4.3 and 5.4 and the protocol is presented in Appendix A2.4. Plots of pollen and spore abundance against time/depth are shown in the respective discussions (Chapters 4 and 5; Figures 4.4. and 5.4).

#### **A3.3.2) Charcoal**

The full charcoal particulate data for Lake Challacaba and Laguna Khomer Kocha Upper is shown in Tables A3.4 and A3.5. A description of the methodology used is provided in Sections 3.4.2, 4.3 and 5.4, and the protocol is presented in Appendix A2.4. Plots of charcoal abundance against time/depth are shown in the respective discussions (Chapters 4 and 5; Figures 4.4. and 5.4).

#### **A3.3.3) Chironomid**

The original data obtained from subfossil chironomid analysis, including percentage and concentration calculations, is provided as an electronic spreadsheet file in Enclosure CD1. Taxa list provided in Appendix A4. The data is divided by study site into the following files:

- Lake Challacaba Chironomid Data.xls
- Laguna Khomer Kocha Upper Chironomid Data.xls

A description of the methodology used is provided in Sections 3.4.3 and 6.4, and the protocol is presented in Appendix A2.4. Plots of chironomid abundance against time/depth are shown in Chapter 6 (Figures 6.4 and 6.5).

Sample code	Depth (cm blf)	Charcoal counts (particulates/cm <sup>3</sup> )				Total
		Type 1 100 – 180 µm	Type 1 >180 µm	Type 2 100 – 180 µm	Type 2 >180 µm	
V2C SS 1cm	1	0	0	0	0	0
V2B SS 11cm	11	1	0	9	1	11
V2B SS 20cm	20	0	0	6	3	9
V2B SS 30cm	30	0	0	2	0	2
V2C SS 40cm	40	0	0	7	0	7
V2B 1 10cm	56	0	0	0	0	0
V2C SS 60cm	60	0	0	17	2	19
V2B 1 15cm	61	1	0	3	0	4
V2B1 20cm	66	0	2	2	0	4
V2B 1 30cm	76	0	0	3	0	3
V2B 1 40cm	86	2	0	5	0	7
V2B 1 50cm	96	4	0	8	0	12
V2B 2 40cm	100	1	0	9	1	11
V2B 2 50cm	110	2	0	40	0	42
V2B 2 60cm	120	7	0	47	9	63
V2B 2 80cm	140	9	4	139	16	168
V2B 2 90cm	150	7	0	153	13	173
V2B 3 30cm	175	1	0	35	10	46
V2B 3 40cm	185	5	0	94	12	111
V2B 3 60cm	205	8	1	81	21	111
V2B 3 70cm	215	8	0	164	14	186
V2B 3 80cm	225	1	4	35	16	56
V2B 3 90cm	235	4	0	159	9	172
V2B 3 99cm	244	4	0	105	7	116
V2B 4 3cm	248	16	1	164	12	193
V2B 4 10cm	255	7	3	146	45	201
V2B 4 20cm	265	5	0	111	21	137
V2B 4 30cm	275	3	0	123	11	137
V2B 4 39cm	284	3	0	55	5	63
V2B 4 50cm	295	0	0	0	0	0

**Table A3.4** Full listing of Lake Challacaba charcoal data. A description of charcoal type morphology is provided in Chapter 3. V2B = core site B. V2C = core site C. SS = from surface sampler.

**Table A3.5 (below and opposite)** Full listing of Laguna Khomer Kocha Upper charcoal data. A description of charcoal type morphology is provided in Chapter 3. KKUA = core site A. KKUB = core site B.

Sample code	Depth (cm blf)	Charcoal counts (particulates/cm <sup>3</sup> )				Total
		Type 1 100 – 180 µm	Type 1 >180 µm	Type 2 100 – 180 µm	Type 2 >180 µm	
KKUA 1 20 cm	51	4	1	49	16	66
KKUA 1 30.5 cm	61.5	11	4	125	23	152
KKUA 1 40 cm	71	23	6	128	48	182
KKUA 1 60 cm	82	31	8	172	54	234
KKUA 1 85 cm	93	17	0	131	33	164
KKUA 1 95 cm	103	28	7	159	37	203
KKUA 2 5 cm	113	22	0	294	53	347
KKUA 2 15cm	123	28	5	301	84	390
KKUA 2 25 cm	133	34	6	289	74	369
KKUA 2 35 cm	143	21	2	183	29	214
KKUA 2 45 cm	153	32	4	246	50	300
KKUA 2 55 cm	163	28	2	179	39	220
KKUA 2 65 cm	173	3	0	57	13	70
KKUA 2 75 cm	183	16	1	234	52	287
KKUA 2 85 cm	193	11	0	108	19	127
KKUA 2 95 cm	203	10	0	124	14	138
KKUB 2 65 cm	205	7	6	143	36	185
KKUB 2 70 cm	210	29	32	631	212	875
KKUB 2 75 cm	215	22	4	146	42	192
KKUB 2 85 cm	225	14	2	162	48	212
KKUA 3 25 cm	233	4	1	188	36	225
KKUA 3 35 cm	243	20	1	435	113	549
KKUA 3 45 cm	253	317	9	522	171	702
KKUA 3 55 cm	263	11	4	648	164	816
KKUA 3 65 cm	273	22	9	614	138	761
KKUA 3 75 cm	283	18	2	251	94	347
KKUA 3 85 cm	293	3	0	187	35	222
KKUA 3 95 cm	303	4	5	314	111	430
KKUA 4 5 cm	313	6	1	101	14	116
KKUA 4 13 cm	320	11	3	599	286	888
KKUA 4 25 cm	331	4	0	159	11	170
KKUA 4 35 cm	340	3	1	128	56	185
KKUA 4 45 cm	349	11	3	212	124	339
KKUA 4 55 cm	358	15	7	230	132	369
KKUA 4 65 cm	367	15	9	148	58	215
KKUA 4 75 cm	376	31	6	322	118	446
KKUA 4 85 cm	385	29	13	351	150	514
KKUA 4 95 cm	394	3	3	74	19	96
KKUA 4 105 cm	403	11	2	87	22	111
KKUA 5 5 cm	413	14	2	67	19	88

KKUA 5 15 cm	423	9	6	33	17	56
KKUA 5 25 cm	433	2	0	5	0	5
KKUA 5 35 cm	443	0	0	15	6	21
KKUA 5 37.5 cm	445.5	2	0	11	2	13
KKUA 5 45 cm	453	0	1	0	0	1
KKUA 5 52 cm	460	4	0	9	2	11

**A3.3.4) Ordination**

The ordination data used to calculate rates of change analysis in Chapters 4 and 5 is shown in Tables A3.6 and A3.7 (overleaf). A description of the ordination methodology is provided in the relevant chapter along with ordination plots and rates of change scores against time/depth.



Sample code	Depth (cm blf)	Sample Age (cal yr BP)	Intersample time (yr)	Non-metric multidimensional scaling (NMDS) axis scores		2 way axis Euclidean distance	Rate of change value
				AXIS 1	AXIS 2		
V2C SS 1cm	1	9.31	N/A	0.73	-0.23	N/A	N/A
V2B SS 11cm	5	46.57	37.25	0.85	-0.30	0.13	0.0008
V2B SS 20cm	10	93.13	46.57	0.65	-0.41	0.23	0.0008
V2B SS 30cm	20	186.26	93.13	0.21	-0.86	0.63	0.0009
V2C SS 40cm	30	279.40	93.13	0.24	-0.55	0.31	0.0012
V2B 1 10cm	50	465.66	186.26	0.82	0.02	0.81	0.0016
V2C SS 60cm	60	558.79	93.13	0.90	0.02	0.09	0.0016
V2B 1 30cm	77	717.12	158.32	0.69	0.18	0.27	0.0017
V2B 1 40cm	87	810.25	93.13	1.07	-0.59	0.87	0.0019
V2B 1 45cm	91	847.50	37.25	1.22	-0.26	0.36	0.0019
V2B 1 50cm	97	923.33	75.83	0.16	-0.55	1.10	0.0028
V2B 2 40cm	100	961.25	37.92	1.01	0.06	1.05	0.0029
V2B 2 50cm	110	1087.64	126.39	-0.10	0.02	1.10	0.0031
V2B 2 60cm	120	1214.03	126.39	-0.10	0.22	0.20	0.0034
V2B 2 70cm	130	1340.42	126.39	-0.21	0.31	0.15	0.0036
V2B 2 80cm	140	1466.81	126.39	-0.98	1.01	1.04	0.0037
V2B 2 90cm	150	1593.19	126.39	-0.39	0.19	1.01	0.0039
V2C 2 55cm	158	1694.31	101.11	-0.63	0.50	0.39	0.0043
V2B 3 30cm	175	1909.17	214.86	-0.52	0.17	0.35	0.0049
V2B 3 40cm	185	2035.56	126.39	-0.51	0.54	0.37	0.0052
V2B3 52cm	197	2187.22	151.67	-0.28	0.03	0.56	0.0055
V2C2 95cm	198	2193.54	6.31	-0.42	0.01	0.14	0.0068
V2B 3 60cm	205	2326.29	132.75	-0.40	-0.72	0.73	0.0073
V2B 3 70cm	215	2515.94	189.65	-0.25	-0.67	0.16	0.0079
V2B 3 80cm	225	2705.58	189.65	-0.50	-0.93	0.36	0.0080
V2B 3 90cm	235	2895.23	189.65	-0.38	-0.41	0.53	0.0082
V2B 3 99cm	244	3065.91	170.68	-0.46	-0.31	0.13	0.0086
V2B 4 3cm	248	3141.77	75.86	-0.27	-0.43	0.24	0.0087
V2B 4 10cm	255	3274.52	132.75	-0.51	-0.40	0.25	0.0093
V2B 4 20cm	265	3464.17	189.65	-0.71	1.09	1.51	0.0097
V2B 4 30cm	275	3653.82	189.65	-0.37	0.16	0.99	0.0145
V2B 4 39cm	284	3824.50	170.68	-1.03	1.47	1.46	0.0223
V2B 4 50cm	295	4033.11	208.61	0.48	1.63	1.51	0.0277

**Table A3.6 (above)** Full listing of the Lake Challacaba ordination data. A description of the ordination methodology is provided in Chapter 4. V2B = core site B. V2C = core site C. SS = from surface sampler.

**Table A3.7 (opposite page)** Full listing of the Laguna Khomer Kocha Upper ordination data. A description of the ordination methodology is provided in Chapter 5. KKUA = core site A. KKUB = core site B.

Sample code	Depth (cm blf)	Sample Age (cal yr BP)	Intersample time (yr)	Detrended correspondence analysis (DCA) axis scores			3 way axis Euclidean distance	Rate of change value
				AXIS 1	AXIS 2	AXIS 3		
KKUA 1 20 cm	51	1024.56	N/A	65.26	19.12	25.78	N/A	N/A
KKUA 1 40 cm	71	1543.52	518.96	48.99	9.95	29.33	19.01	0.0366
KKUA 1 60 cm	82	1900.17	356.65	48.12	19.85	15.88	16.73	0.0469
KKUA 1 85 cm	93	2256.82	356.65	53.96	26.31	27.64	14.64	0.0410
KKUA 1 95 cm	103	2581.04	324.23	50.77	37.12	30.64	11.66	0.0360
KKUA 2 5 cm	113	2905.27	324.23	35.23	20.90	5.50	33.71	0.1040
KKUA 2 15cm	123	3229.50	324.23	32.06	0.00	35.98	37.10	0.1144
KKUA 2 25 cm	133	3622.83	393.33	32.68	7.46	29.71	9.76	0.0248
KKUA 2 35 cm	143	4016.17	393.33	51.78	27.15	23.01	28.24	0.0718
KKUA 2 45 cm	153	4409.50	393.33	36.07	10.26	32.20	24.83	0.0631
KKUA 2 55 cm	163	4802.83	393.33	26.58	1.87	34.64	12.90	0.0328
KKUA 2 65 cm	173	5196.17	393.33	28.06	5.75	15.84	19.25	0.0490
KKUA 2 75 cm	183	5589.50	393.33	42.70	8.60	34.81	24.13	0.0613
KKUA 2 85 cm	193	5982.83	393.33	25.36	5.80	8.00	32.05	0.0815
KKUA 2 95 cm	203	6376.17	393.33	45.57	12.31	20.75	24.77	0.0630
KKUB 2 65 cm	205	6454.83	78.67	20.63	9.61	32.85	27.85	0.3540
KKUB 2 75 cm	215	6687.58	232.75	13.20	6.27	29.30	8.89	0.0382
KKUB 2 85 cm	225	6759.75	72.17	13.89	11.99	58.79	30.04	0.4163
KKUA 3 25 cm	233	6817.49	57.74	16.59	8.19	0.30	58.68	1.0163
KKUA 3 35 cm	243	6889.66	72.17	35.85	54.14	24.76	55.50	0.7691
KKUA 3 45 cm	253	6961.83	72.17	9.18	12.07	0.00	55.63	0.7708
KKUA 3 55 cm	263	7034.00	72.17	23.31	26.39	35.38	40.70	0.5640
KKUA 3 65 cm	273	7350.98	316.98	6.48	21.04	15.49	26.60	0.0839
KKUA 3 75 cm	283	7667.97	316.98	40.45	56.56	22.05	49.58	0.1564
KKUA 3 85 cm	293	7984.95	316.98	0.33	29.22	26.85	48.79	0.1539
KKUA 3 95 cm	303	8301.93	316.98	9.08	25.76	43.09	18.77	0.0592
KKUA 4 5 cm	313	8618.91	316.98	33.89	67.31	5.45	61.31	0.1934
KKUA 4 25 cm	331	9005.47	386.56	14.48	27.38	63.04	72.71	0.1881
KKUA 4 35 cm	340	9125.15	119.68	15.54	38.56	25.78	38.91	0.3252
KKUA 4 45 cm	349	9244.82	119.68	33.39	64.79	48.06	38.77	0.3239
KKUA 4 55 cm	358	9364.50	119.68	9.34	30.20	19.30	51.01	0.4262
KKUA 4 65 cm	367	9482.33	117.83	20.15	19.08	43.78	28.97	0.2459
KKUA 4 75 cm	376	9600.17	117.83	0.00	20.90	8.28	40.86	0.3468
KKUA 4 85 cm	385	9718.00	117.83	16.96	77.34	25.20	61.31	0.5203
KKUA 4 95 cm	394	10727.49	1009.49	14.69	46.15	11.07	34.32	0.0340
KKUA 4 105 cm	403	11736.98	1009.49	41.98	43.84	31.84	34.37	0.0340
KKUA 5 5 cm	413	12858.63	1121.65	35.84	32.09	23.75	15.53	0.0138
KKUA 5 15 cm	423	13980.28	1121.65	66.50	64.53	30.23	45.10	0.0402
KKUA 5 25 cm	433	15101.93	1121.65	90.00	17.68	36.82	52.82	0.0471
KKUA 5 35 cm	443	16223.59	1121.65	87.72	34.91	18.48	25.27	0.0225
KKUA 5 45 cm	453	17345.24	1121.65	66.20	0.44	35.53	44.06	0.0393
KKUA 5 50 cm	458	17906.07	560.83	73.60	1.35	24.69	13.16	0.0235



Appendix A4) Identified ecological remains

This appendix presents details of the fossil pollen, spore, algal and chironomid types identified from the analysis of the Lake Challacaba and Laguna Khomer Kocha Upper sediments cores. Pollen, spore and algal images are provided on the enclosed CD (Enclosure CD1).

A4.1) Pollen, spore and algal types

A list of the fossil pollen, spore and algal taxa identified from the analysis of the Lake Challacaba and Laguna Khomer Kocha Upper sediments cores are given in Tables A4.1 and A4.2. In addition, a total of 80 unknown taxa (Unknown 1–80), which only had minimal occurrences, were identified. Twenty-four of these unknowns where later identified to family/genus level. Photographs of the taxa (including the unknowns) are provided in the Enclosure CD1.

Spore types		Algal types
Isoëtes type 1	Spyra Gyra (HHT 375/374)	Pediastrum duplex type
Isoëtes type 2	Sporormiella	Pediastrum simplex type
Joined spore	Trilete type 1	Pediastrum mini type
Neurospora HHT361	Trilete type 2	
Monolete Psilate	Trilete type 3	
Monolete Verrucate	Trilete type 4	
Monolete type 1	Trilete type 5	
Monolete type 2	Trilete type 6	
Monolete type 3	Trilete type 7	
Monolete type 4	Trilete type 8	
Monolete type 5	Trilete type 9	
Monolete type 6	Trilete type 10 - Lycopodium	
Monolete type 7	Trilete type 11	
Rugby-ball shaped spore	Trilete type 12	
Rugby-ball shaped (smooth) spore	Trilete type 13	
Spore HHT 354		

Table A4.1 Spore and algal taxa identified from Lake Challacaba and Laguna Khomer Kocha Upper sediment cores.

Family	Genus/Type	Family	Genus/Type	Family	Genus/Type
Alismataceae	<i>Sagittaria</i> Type 1	Ericaceae	Type 1	Moraceae / Urticaceae	Type 5
	<i>Sagittaria</i> Type 2	Euphorbiaceae	<i>Acalypha</i> Type 1		Type 6
	<i>Sagittaria</i> Type 3		<i>Acalypha</i> Type 2		Type 7
Amaranthaceae	Type 1 c.f. <i>Gomphrena</i>		<i>Acalypha</i> Type 3		Type 8
	Type 2		Un. Diff. Type 1	Myrsinaceae	Type 1 c.f. <i>Rapanea</i>
	Type 3 c.f. <i>Pfaffia</i>		Un. Diff. Type 2	Myrtaceae	<i>Eucalyptus</i> Type 1
	Type 4 c.f. <i>Alternanthera</i>		Un. Diff. Type 4		Type 2
	Type 5		Un. Diff. Type 5	Onagraceae	<i>Ludwigia</i> Type 1
Anacardiaceae	<i>Astronium</i> Type 1		Un. Diff. Type 6	Oxalidaceae	<i>Oxalis</i> Type 1
	Type 2		Type 7 c.f. <i>Alchornea</i>	Papaveraceae	Type 1 c.f. <i>Bocconia</i>
Apiaceae	<i>Hydrocotyle</i> Type 1	Fabaceae – Mimosoideae	Type 8 c.f. <i>Alchornea</i>		Type 2
	Type 2		Type 1 c.f. <i>Inga</i>	Piperaceae	<i>Piper</i> Type 1
	Type 3 c.f. <i>Myrrhidendron</i>		Type 2	Plantaginaceae	<i>Plantago</i>
	Type 4 c.f. <i>Eryngium</i>		Type 3	Poaceae	Type 1
Apocynaceae	Type 1		Type 4	Podocarpaceae	<i>Podocarpus</i> Type 1
Asteraceae	Type 1		Type 5	Rosaceae	<i>Polylepis/Acaena</i> Type 1
	Type 2		Type 6 c.f. <i>Mimosa</i>		<i>Polylepis/Acaena</i> Type 2
	Type 3		Type 7 c.f. <i>M. acerba</i>		<i>Polylepis/Acaena</i> Type 3
	Type 4	Flacourtiaceae	Type 1		<i>Polylepis/Acaena</i> Type 4
	Type 5		Type 2	Ranunculaceae	<i>Thalictrum</i> Type 1
Betulaceae	<i>Alnus</i> Type 1	Gunneraceae	<i>Gunnera</i> Type 1	Rubiaceae	Type 2
	<i>Alnus</i> Type 2	Haloragaceae	<i>Myriophyllum</i>		Type 1 c.f. <i>Borreria</i>
Brassicaceae	Type 1	Juglandaceae	<i>Juglans</i> Type 1		Type 2
	Type 2		Type 2		Type 3 c.f. <i>Cupania</i>
	Type 3	Lamiaeae	Type 1		Type 4
	Type 4	Lemnaceae	<i>Lemna</i> Type 1		Type 5
Bromeliaceae	Type 1		<i>Lemna</i> Type 2		Type 6
	Type 2		<i>Lemna</i> Type 3	Sapindaceae	Type 1
Buxaceae	Type 1 c.f. <i>Styloceras</i>	Loganiaceae	Type 1 c.f. <i>Strychnos</i>	Solanaceae	Type 1
Caryophyllaceae	Type 1	Lythraceae	Type 1 c.f. <i>Cuphea</i>		Type 2
Chenopodiaceae	Type 1	Malvaceae	Type 1		Type 3
/	Type 2	Melastomataceae / Combretaceae	Type 1		Type 4
	Type 3		Type 2		Type 5
Chloranthaceae	<i>Hedyosmum</i> Type 1		Type 3	Typhaceae	<i>Typha</i> Type 1
Cunoniaceae	<i>Weinmannia</i> Type 1	Moraceae/ Urticaceae	<i>Cecropia</i> Type 1		<i>Typha</i> Type 2
Cyperaceae	Type 1		Type 2	Ulmaceae	<i>Trema micrantha</i> Type 1
	Type 2		Type 3		<i>Celtis</i> Type 2
Ephedraceae	<i>Ephedra</i> Type 1		Type 4		<i>Celtis</i> (triangular) Type 3

Table A4.2 Pollen taxa identified from Lake Challacaba and Laguna Khomer Kocha Upper sediment cores.



A4.2) Chironomid types

A list of the subfossil chironomid taxa identified from the analysis of the Lake Challacaba and Laguna Khomer Kocha Upper sediments cores is given in Table A4.3. Line drawings, photographs and taxonomic notes of the subfossil chironomid taxa are provided in Chapter 6.

Family	Subfamily	Tribe	Genus
Chironomidae	Chironominae	Chironomini	Chironomus
			Parachironomus
		Tanytarsini	Tanytarsus
	Tanypodinae	Macropelopiini	Apsectrotanypu
	Orthoclaadiinae		Cricotopus / Orthocladius type I
			Cricotopus / Orthocladius type II
			Limnophyes / Paralimnophyes
			Paracricotopus
			Smittia / Paramittia
			Pseudosmittia

Table A4.3 Chironomid taxa identified from Lake Challacaba and Laguna Khomer Kocha Upper sediment cores.